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STRUCTURE ET DIVERSITÉ FONCTIONNELLE DES COMMUNAUTÉS D'ARTHROPODES DE LA LITIÈRE FORESTIÈRE

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RÉSUMÉ

L'approche par traits fonctionnels est bien implantée dans l'étude de l'écologie végétale, mais demeure plus marginale en écologie animale. Le principe de l'approche fonctionnelle est de relier les traits (morphologiques, physiologiques, phénologiques ou comportementaux) des organismes à des gradients environnementaux ou des processus écosystémiques dans l'optique d'identifier les mécanismes impliqués. Depuis quelques années, un intérêt grandissant pour l'étude des traits fonctionnels des animaux s'est développé pour répondre à des questions sur la structure des réseaux trophiques et leur impact sur les services écosystémiques. L'objectif de cette thèse est d'identifier des traits fonctionnels des macroarthropodes de la litière forestière permettant de prédire leurs interactions et voir comment ces traits sont distribués dans l'espace. Une importance particulière a été accordée aux traits reliés à l'alimentation. La première étape a été d'effectuer une revue de littérature sur l'utilisation de l'approche par traits fonctionnels chez les arthropodes terrestres qui a révélé plusieurs lacunes. Premièrement, dans plusieurs publications, il y a un manque de transparence dans l'élaboration des hypothèses. De façon plus générale, il y a un manque de cohésion entre les études limitant grandement les généralisations. Nous y présentons un cadre de travail, provenant de la littérature sur les végétaux, pour élaborer des hypothèses permettant d'identifier les mécanismes impliqués dans l'assemblage des communautés (traits réponses) et les processus écosystémiques (traits effets). De plus, nous suggérons une plus grande inclusion de traits liés à la biomécanique et généralisables à un large éventail de taxa en prenant comme exemple les traits d'alimentation. L'objectif du deuxième chapitre était de créer un modèle prédictif des interactions prédateurs/ proies en ce basant sur leurs traits respectifs et leur phylogénie. Une expérience a été réalisée durant laquelle 20 espèces de carabes étaient mises en présence d'une grande variété de proies (une à une) pour déterminer s'il y avait une interaction entre elles. Des traits comme la taille du prédateur et de la proie, la force des mandibules du prédateur et la dureté de la cuticule de la proie ont été utilisés pour construire le modèle. Ces traits permettent de prédire correctement ~76 % des interactions (réalisées et non réalisées combinées) des carabes, mais ne permettent pas de bien prédire les interactions non réalisées. Par contre, l'introduction d'une composante phylogénétique, agissant hypothétiquement comme une approximation pour des traits non mesurés comme les défenses chimiques, améliore grandement la prédiction des interactions non réalisées. Au final, le modèle prédit correctement ~80 % des interactions. Dans le chapitre 3, nous nous intéressons à la distribution dans l'espace des traits d'alimentation des décomposeurs et des prédateurs vivant dans la litière forestière et comment ils covarient avec les facteurs abiotiques et les traits de palatabilité des ressources. Les macroarthropodes

ont été échantillonnés dans 110 parcelles réparties dans trois sites du sud du Québec. Les diplopodes, isopodes (décomposeurs), araignées, opilions et carabes (prédateurs) ont été identifiés à l'espèce. Les traits de palatabilité ont été mesurés pour les feuilles de la litière (épaisseur, dureté, rétention en eau) et les proies (taille, largeur, dureté), et les traits d'alimentation pour les décomposeurs et prédateurs (taille, force et taille des pièces buccales). Les résultats montrent que les traits d'alimentation des décomposeurs et des prédateurs covarient avec les facteurs abiotiques (température et humidité) du milieu. De plus, les traits d'alimentation des consommateurs et de palatabilité des proies covarient conjointement dans l'espace. Les résultats de cette thèse démontrent le potentiel que représente l'étude des traits fonctionnels des arthropodes pour comprendre la dynamique des réseaux trophiques et l'assemblage des espèces. De plus des traits généralisables à une grande variété de taxa comme la force des pièces buccales et la dureté de la cuticule ont été identifiés. Quelques lacunes/ limitations de l'approche sont également mises en lumière; ces aspects devront être considérés dans les prochaines années pour rendre l'approche pleinement fonctionnelle.

Mots clés: Traits fonctionnelles, arthropodes, réseaux trophiques, interactions prédateurs/ proies

INTRODUCTION

Le sol forestier soutient un réseau trophique complexe et diversifié composé de champignons, bactéries, amibes, flagellés, nématodes, gastéropodes, annélides, arthropodes et petits vertébrés (Maraun et al. 2001, Coleman et al. 2004). Les interactions entre ces différents organismes ont un impact plus ou moins direct sur les processus de décomposition et de minéralisation des nutriments (de Vries et al. 2013). Démêler l'ensemble de ces interactions et quantifier leur importance est une tâche hautement complexe, mais nécessaire pour comprendre et prédire leur dynamique (Gravel et al. 2016).

L'écologie en générale est dans un besoin de développer une approche plus prédictive, particulièrement dans le contexte mondial des changements globaux (McGill et al. 2006, Kerr et al. 2007, Woodward et al. 2010). Dans le cas de l'écologie du sol, où la diversité est très élevée avec de nombreuses espèces microscopiques et où la majorité des interactions s'effectuent de façon cryptique, les outils prédictifs pourraient aussi aider à identifier les interactions interspécifiques (Morales-Castilla et al. 2015). Un outil potentiel souvent évoqué est l'approche par traits fonctionnels (McGill et al. 2006, Morales-Castilla et al. 2015, Gravel et al. 2016). Par contre, cette approche a principalement été développée avec les plantes et est encore en cours de développement pour les autres organismes.

Diversité et décomposition

La décomposition est un processus écologique de base dans le cycle des nutriments durant lequel les matières végétales sont humifiés, alors que plusieurs nutriments tels

que l'azote (N) et le carbone (C) sont minéralisés (Coûteaux et al. 1995). En milieu forestier, plus de 80 % du matériel végétal n'est pas consommé par les herbivores et doit être décomposé (Cebrian 1999). Les feuilles représentent la part la plus importante des débris végétaux au sol (Gessner et al. 2010). Les microbes (bactéries et champignons) sont les organismes les plus diversifiés du sol avec au-delà de 26000 espèces par gramme de sol dans le sol forestier (Roesch et al. 2007). Ils sont les principaux responsables de la dégradation de la matière organique et du retour des nutriments aux plantes (Coleman et al. 2004). Les microbes représentent également la principale source de nourriture de plusieurs membres de la microfaune (amibes, rotifères, nématodes) et de la mésofaune (collemboles, acariens).

L'activité des animaux bactériophages et fongivores a un impact sur la minéralisation des nutriments. Par exemple, les collemboles et les nématodes fongivores peuvent avoir un effet positif sur la quantité de N disponible dans le sol en stimulant la croissance des champignons (Chen et Ferris 1999, Cragg et Bardgett 2001, Filser 2002). Ces effets vont varier selon les espèces en présence, mais les mécanismes au-delà des préférences spécifiques (broutage spécifique) (Cragg et Bardgett 2001, Crowther et A'Bear 2012) sont mal connus.

La macrofaune est constituée principalement d'arthropodes, annélides et gastéropodes. Traditionnellement, leur rôle dans la décomposition est perçu comme étant relié à la fragmentation de la litière (Van Der Drift 1951, Coleman et al. 2004, David et Handa 2010), mais ce rôle est maintenant contesté (David 2014) puisque leurs boulettes fécales ne semblent pas se décomposer plus rapidement que la litière non consommée (Nicholson et al. 1966, Rawlins et al. 2007, Frouz et Šimek 2009). Cependant, ces études ont été réalisées sur les boulettes fécales de peu d'espèces de décomposeurs généralement nourris sur des feuilles provenant d'une seule espèce d'arbre. De plus, l'intégrité structurelle des boulettes fécales était conservée; i.e. elles n'ont pas été écrasées ou fragmentées ce qui ne favorise pas une maximisation de la

surface de contact des fragments végétaux. Par ailleurs, une étude récente démontre que dans certains cas, les fèces peuvent se décomposer plus rapidement que la litière, en fonction des transformations chimiques subies durant la digestion, mais les causes exactes ne sont pas claires (Coulis et al. 2016).

Quoi qu'il en soit, les macro-détritivores ont généralement un impact favorable sur la flore microbienne en stimulant leur activité dans les fèces fraîches (Rawlins et al. 2007), en relâchant de l'azote (N) sous forme d'ammonium dans leurs déjections (Cárcamo et al. 2000) et en fracturant les cellules de la litière en la consommant (Frouz et Šimek 2009). L'apport des fèces dépend à la fois de la nourriture consommée (Coulis et al. 2016) et des caractéristiques d'ingestion et de digestion des consommateurs (Frouz et Šimek 2009). Des différences importantes sont observées entre les grands groupes taxonomiques (e.g. les fèces de vers de terre sont plus riches en C que ceux des mille-pattes (Hedde et al. 2007)), mais aussi entre des espèces proches évolutivement (Hedde et al. 2007, Frouz et Šimek 2009, Coulis et al. 2015). Les fèces de décomposeurs ont un intérêt particulier puisqu'ils représentent un lien direct avec les microbes. L'impact des fèces sur les microbes, et la décomposition en général, va dépendre de ces caractéristiques telles le ratio C:N, le degré de fragmentation des débris végétaux et leur compaction (Hedde et al. 2007, Frouz et Šimek 2009, David 2014, Coulis et al. 2015). Les déjections des prédateurs vivant dans la litière forestière et leur impact sur la flore microbienne ne semblent pas avoir été étudiées. Par contre, les fèces des prédateurs sont connues pour être très riches en N (Romero et al. 2006) et donc devraient être favorables à l'activité bactérienne à court terme tout en possédant très peu d'éléments récalcitrants. Particulièrement, le N est sous forme de guanine dans les fèces d'araignées (Schmidt et al. 1955), un aminoacide facilement absorbable.

Les exemples présentés dans cette section font le lien entre les différents niveaux trophiques de façon linéaire. Ce genre d'observation est nécessaire pour comprendre

les interactions de base et le fonctionnement des écosystèmes. Dans la réalité, les interactions ne sont pas linéaires. Par exemple, les macroarthropodes n'utilisent généralement pas la litière fraîche préférant la litière prédécomposée et conditionnée par les microbes (Wolters 2000, De Oliveira et al. 2010, David 2014). Pour pouvoir comprendre et prédire la dynamique des écosystèmes et son impact sur les processus comme la décomposition, il est important d'étudier les systèmes dans leur entière complexité (Duffy et al. 2007).

Réseaux trophiques du sol

Une façon simplifiée de voir la décomposition est de considérer que trois niveaux trophiques sont directement impliqués; les plantes fournissant le matériel de base, les microbes et les décomposeurs. À ceux-ci s'ajoutent les prédateurs qui ne sont pas directement impliqués dans la décomposition. Plusieurs études démontrent qu'augmenter la diversité à un ou l'autre des niveaux trophiques peut augmenter la vitesse de décomposition: diversité des plantes (Hector et al. 2000, Pérez Harguindeguy et al. 2008), diversité des microbes (Bell et al. 2005, Gravel et al. 2011), diversité des décomposeurs (Srivastava et al. 2009, Handa et al. 2014). Par contre, plusieurs résultats contradictoires sont également observés (Griffiths et al. 2000, Bonanomi et al. 2010, Coq et al. 2011, Eisenhauer et al. 2011). Pour expliquer ces résultats contradictoires, plusieurs ont émis l'hypothèse que la diversité fonctionnelle à un plus grand impact que la diversité spécifique sur la vitesse de décomposition (McTiernan et al. 1997, Heemsbergen et al. 2004, Hättenschwiler et al. 2005, Schimel et Hattenschwiler 2007, Hättenschwiler et al. 2011). Par diversité fonctionnelle, ont entend la diversité des traits (caractéristiques phénologiques, physiologiques et comportementales) des organismes représentée dans une communauté (Violle et al. 2007, Pey et al. 2014b) (voir section suivante).

En théorie, une augmentation de la diversité devrait avoir un impact positif sur le rendement des processus écologiques en favorisant la complémentarité entre les espèces (Loreau et al. 2001). La complémentarité peut s'exprimer de deux façons: 1) par une séparation de niche favorisant une meilleur utilisation des ressources disponibles (e.g. une variation dans la température optimale d'activités entre les espèces d'abeilles augmentent le taux de fleurs pollinisé (Fründ et al. 2013); 2) par un processus de facilitation (De Oliveira, Haettenschwiler & Handa 2010). Cependant, la majorité des études ont été réalisées sur un seul niveau trophique (mais voir Naeem et al. 1994). Déterminer l'impact des changements de diversités à plusieurs niveaux trophiques peut être difficile puisque plusieurs méchanismes sont impliqués (Duffy et al. 2007). D'une façon générale, il faut s'attendre à ce qu'une augmentation de la diversité à un niveau tropique augmente l'utilisation des ressources à niveau précédent (Loreau 2010). L'impact sur le niveau inférieur est difficilemet prévisible, mais l'impact devrait être de moins en moins fort sur les niveaux subséquent; donc plus le niveau trophique est éloigné du processus étudié, moins sa diversité fonctionnelle devrait l'affecter (Loreau 2010).

Peu d'études ont étudié simultanément la diversité (spécifique ou fonctionnelle) à plus d'un niveau trophique dans la décomposition, mais le peu de résultats sur le sujet semble démontrer un impact positif de la diversité des décomposeurs (Handa et al. 2014). Un impact de la diversité des décomposeurs sur la décomposition est plus probable si on considère un système naturel où les feuilles présentent dans la litière possèdent des traits et des stades de décomposition différents; dans un tel scénario, une utilisation différente des ressources par différentes espèces de décomposeurs risque d'accélérer la vitesse de décomposition. Il ne semble pas que cette hypothèse ait été testée jusqu'à présent. Les études mettant en relation des décomposeurs avec des types d'alimentation différents tendent à démontrer un effet synergétique sur la vitesse de décomposition (Hättenschwiler et Gasser 2005, Zimmer et al. 2005, Partsch et al. 2006, De Oliveira et al. 2010, Coulis et al. 2015). L'impact de la

diversité des prédateurs n'a quant à lui jamais était formellement étudié, mais certains résultats semblent démontrer que l'impact des prédateurs dépend avant tout des proies utilisées (Lawrence et Wise 2004, Schmitz et al. 2010).

Les interactions réalisées jouent un rôle important dans la vitesse de décomposition et la diversité a probablement un effet positif sur la décomposition en favorisant la diversification des interactions réalisées (Kardol et al. 2016). Cependant, identifier les interactions dans le réseau trophique du sol peut représenter un défi majeur en considérant la diversité spécifique (et la difficulté taxonomique qu'elle représente), la petite taille de plusieurs espèces et les interactions souvent cryptiques (Brose et Scheu 2014). Tout de même, différents réseaux trophiques du sol ont été décrits (Scheu 2002, Berg et Bengtsson 2007, Holtkamp et al. 2008), mais les liens sont souvent grossiers, i.e. ils sont décrits entre des groupes taxonomiques ou des guildes larges (bactéries, nématodes omnivores, acariens prédateurs, collemboles), plutôt qu'entre les espèces. Ce manque de résolution taxonomique peut créer un biais d'interprétation en ayant une influence sur la structure et les propriétés des réseaux trophiques (Sechi et al. 2015). Récemment, Digel et al. (2014) ont publié le réseau trophique du sol de 16 forêts en Allemagne en ce basant à la fois sur des tests d'alimentation, des données moléculaires et isotopiques, des traits écologiques et des relations allométriques de taille. Ces deux derniers points sont particulièrement intéressants puisqu'ils reflètent deux aspects déterminant la probabilité d'interactions entre deux espèces: la probabilité d'une rencontre et le couplage des traits du prédateur et de la proie (Gravel et al. 2016). Développer des outils prédictifs pour les interactions est nécessaire pour pouvoir étudier les réseaux trophiques à large échelle et pour prédire l'impact des introductions et des pertes d'espèces dans les écosystèmes; les traits fonctionnels pourraient aider à répondre à ce besoin (Gravel et al. 2013, Morales-Castilla et al. 2015, Gravel et al. 2016).

Traits fonctionnels des arthropodes

L'approche par traits fonctionnels a principalement été développée avec les végétaux (Lavorel et al. 2007, Violle et al. 2007, Garnier et al. 2016) et repose sur deux principes de bases: les "traits réponses" des organismes déterminent leur capacité de survie et de reproduction dans un milieu en fonction de ses caractéristiques abiotiques et biotiques (Keddy 1992); les "traits effets" des organismes déterminent leur impact sur les processus écosystémiques (Chapin et al. 2000). L'approche par traits fonctionnels présente une capacité de généralisation plus grande que l'approche taxonomique traditionnelle et facilite l'identification des mécanismes menant à l'assemblage des espèces et déterminant les processus écosystémiques (McGill et al. 2006, Shipley 2010, Laughlin 2014).

Chez les animaux, les traits fonctionnels ont été étudiés dans un grand nombre de groupes incluant les mammifères (Davies et al. 2007), les oiseaux (Croci et al. 2008), les poissons (Mouillot et al. 2013), les invertébrés aquatiques (Poff et al. 2006) et du sol (Hedde et al. 2012), les nématodes (Schratzberger et al. 2007), etc. Cependant, peu d'études ont tenté d'uniformisé l'approche fonctionnelle avec les animaux en tenant compte de leurs particularités d'hétérotrophes (Luck et al. 2012, Pey et al. 2014b, Fountain-Jones et al. 2015). Une exception notable est chez les macro-invertébrés aquatiques (Usseglio-Polatera et al. 2000, Bêche et al. 2006, Poff et al. 2006), pour lesquels une culture de classification des organismes en fonction de leur trait est plus ancienne (Cummins 1973). Le cas des arthropodes terrestres pose un problème particulier de par leur grande diversité spécifique, de forme et de niche. Plusieurs études ont utilisé l'approche par traits fonctionnels avec les principaux taxa comme les acariens (Maaß et al. 2015, Mori et al. 2015), araignées (Bonte et al. 2006, Podgaiski et al. 2013), collemboles (Malmstrom 2012, Santorufo et al. 2014), orthoptères (Dziock et al. 2011, Deraison et al. 2015), coléoptères (Ribera et al. 2001, Watts et Mason 2015) abeilles (Hoehn et al. 2008, Fründ et al. 2013), etc., mais une

approche collective généralisable à l'ensemble des taxa est toujours manquante. L'approche par traits fonctionnels avec les arthropodes a principalement été utilisée pour décrire leur réponse à différentes perturbations (Arnan et al. 2013, Hedde et al. 2013, Bachand et al. 2014) et dans quelques cas, pour décrire leur impact sur les processus écosystémiques (Heemsbergen et al. 2004, Fründ et al. 2013, Munyuli 2014, Coulis et al. 2015).

Un aspect intéressant, mais moins étudié, est l'utilisation du couplage de traits entre différentes espèces pour décrire ou prédire leurs interactions potentielles (Rohr et al. 2016). L'intérêt est d'identifier les traits des ressources qui vont imposer une contrainte sur les traits d'alimentation du consommateur. Par exemple, la longueur de la langue d'une abeille va déterminer les fleurs potentiellement utilisées en fonction de la profondeur de la corolle (Ibanez 2012). Chez les oiseaux frugivores, la taille du bec détermine la taille des fruits consommés (Dehling et al. 2014), ce qui à un impact sur la taille des graines dispersées par l'oiseau (Moran et Catterall 2010). Chez les prédateurs, le ratio taille du prédateur / taille de la proie est un couplage de trait important souvent étudié (Brose et al. 2006, Gravel et al. 2013). Les demandes énergétiques peuvent également contraindre les interactions; ainsi, les poissons à nage rapide et à haute demande énergétique ont tendance à privilégier des proies avec une haute teneur calorique et lipidique (Spitz et al. 2014). Finalement, des traits biomécaniques comme la force des pièces buccales peuvent également contraindre la dureté des plantes utilisées par les herbivores (Ibanez et al. 2013). Par contre, les études sur le couplage de traits avec les arthropodes se limitent aux groupes herbivores (Inouye 1980; Kunte 2007; Ibanez 2012; Ibanez et al. 2013; Deraison et al. 2015; Stavert et al. 2016) et les traits d'alimentation et de vulnérabilité dans les relations prédateurs/ proies sont moins bien connu. De plus, jusqu'à très récemment (Le Provost et al. 2017), aucune études n'avais analysée si les variation dand les valeur de traits entre les communités d'un niveau trophique pouvais déterminé les variation de valeur de traits aux autres niveaux trophiques.

Objectifs

L'objectif de cette thèse est d'identifier des traits fonctionnels des macroarthropodes de la litière forestière permettant de prédire leurs interactions et voir comment ces traits sont distribués dans l'espace. Une importance particulière a été accordée aux traits reliés à l'alimentation puisqu'ils sont directement reliés aux interactions interspécifiques et que cet aspect a été rarement traité dans la littérature avant le début de ma thèse en 2011: depuis quelques travaux s'y sont attardés (e.g. Ibanez et al. 2013, Deraison et al. 2015). Idéalement, l'ensemble des intéractions (i.e. alimentaire, compétition, abiotique, etc.) devraient être analysées pour déterminer l'importance relative de chaque. Par contre, les connaissances actuelles ne permettent pas de la faire sans inclure des expérimentations pour bien identifier les traits pertinents pour représenter adéquatement chaque type d'interactions. Les traits d'alimentations ont été prévilégiés, car ils sont directement relié à l'utilisation des ressources (donc relié à la compétition), et sont mieux connu dans la littérature sur la morphologie fonctionnelle des arthropodes.

Le chapitre 1 est une revue de la littérature critique sur l'utilisation de l'approche par traits fonctionnels avec les arthropodes terrestres. L'objectif premier était de faire une synthèse des différents traits utilisés dans la littérature et de voir comment ils étaient reliés aux filtres environnementaux. Cette revue a permis de mettre en lumière certains problèmes reliés à l'application de l'approche avec les arthropodes affectant particulièrement le potentiel de généralisation de certains résultats. En ce basant sur les bases posées par nos prédécesseurs dans l'étude des traits des arthropodes et en écologie végétale, il y est proposé des recommandations quant à la sélection des traits étudiés et sur la généralisation des traits entre taxa. Entre autres, il est suggéré d'accorder une plus grande place aux traits biomécaniques en présentant des exemples reliés aux traits d'alimentation. Ce chapitre est en révision et sera resoumis au cours de l'automne à *Journal of Animal Ecology*.

L'objectif dans le chapitre 2 est de développer un modèle prédictif les interactions prédateurs-proies basé sur les traits fonctionnels et la phylogénie. L'hypothèse de départ était que l'occurence des interactions est déterminé par le couplage des traits d'alimentation des prédateurs et des traits de palatabilité des proies. Par exemple, la taille des prédateurs est couplée à la taille des proies et la force des mandibules des prédateurs est couplée à la dureté de la cuticule des proies. De plus, la phylogénie est introduite pour tenir compte de traits comme les défenses chimiques des proies qui ont un effet dissuasif sur certains prédateurs, mais qui sont difficiles à documenter et à introduire dans un principe de couplage de traits. L'hypothèse sous-jacente est que les espèces proches évolutivement vont avoir des interactions avec les même groupes d'espèces. Une expérience d'alimentation impliquant 20 espèces de carabes a été effectuée pour récolter les données d'interactions. Cette approche nous permet d'obtenir des informations sur les interactions réalisées, mais également sur celles non réalisées, ce qui permet de mieux cerner les contraintes d'interactions entre prédateurs et proies. Des données d'interactions provenant de la littérature ont également été utilisées. Ce chapitre sera bientôt soumis à *Functional Ecology*.

Le troisième chapitre est une étude sur la covariation des traits d'alimentation des macroarthropodes de la litière forestière avec les caractéristiques abiotiques et les traits de palatabilité de leur ressource. Les traits de bases étudiés sont très similaires à ceux utilisés dans le chapitre 2, mais appliqué à une plus grande diversité de taxa. L'hypothèse est que les traits de palatabilité des ressources vas influencer la distribution d'alimentation des consommateurs ce qui va résulter en une covariation des traits des ressources et des consommateurs dans l'espace. La covariation des traits est étudiée pour deux niveaux d'interactions: décomposeurs-litière et prédateurs-proies. Les macroarthropodes ont été échantillonnés dans 110 parcelles réparties dans trois sites du sud du Québec. Le groupe des décomposeurs est constitué des

diplopodes et des isopodes, les prédateurs par les carabes, araignées et opilions et les proies par les décomposeurs, larves et autres macroarthropodes.

CHAPITRE 1

ON THE DEVELOPMENT OF A FUNCTIONAL TRAIT APPROACH FOR TERRESTRIAL ARTHROPODS

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1.1 Abstract

The characterization of ecological communities with functional traits allows to consider simultaneously the ability of a species to survive and reproduce in an environment, its interactions with other species, and its effects on the ecosystem. Despite its recent popularity in community ecology and biogeography, functional traits have been studied mainly by plant ecologists. Trait-based studies for other taxa, including arthropods, remain marginal. Arthropods represent a group for which a functional trait approach could be highly profitable because of their high diversity, abundance, ubiquity and role in many important ecological processes. The literature review shows that the approach is often used in the absence of a clear hypothesis-driven approach which limits generalizations and the ability to identify ecological mechanisms. To palliate these problems, we propose a step-by-step protocol to postulate clear hypothesis before selecting response or effect traits to studies and integrate more generalizable traits. The functional approach with arthropods would benefit of the development of a list of traits determining interspecific interactions. We present the concept of trait-matching with several examples of arthropods traits known to be effective predictor of their interactions. Including the concept of trait-matching in functional approach with arthropods could help answer questions related to response and effect traits. The development of a successful functional trait approach for terrestrial arthropods will necessitate an understanding of relevant traits, standardized measurement protocols and open access databases to share this information. Such progress will provide ecologists with a new set of tools to answer broad questions in several fields including the study of community assembly, ecological networks and multi-trophic functionality.

1.2 Introduction

The use of traits to understand the relationship of an organism to its environment has been fundamental to ecology. While early studies on traits were limited to qualitative assessments of community structure (e.g. Raunkiær 1934), a new generation of studies is building on a wide range of quantitative indices (Mouillot et al. 2013), providing a more predictive approach (Webb et al. 2010) and allowing for a greater emphasis on understanding functions within ecosystems (Lavorel 2013). A "trait" refers to any morphological, physiological, phenological or behavioural characteristic measurable at the individual level (Violle et al. 2007; Pey et al. 2014b). "Functional traits" are "traits" either related to the performance (growth rate, survival or reproduction probability) of the organism (response traits), to an ecological process (effect traits) (Violle et al. 2007), or in some cases, to both (Lavorel et al. 2013). While taxonomic studies typically describe changes in community composition, functional trait studies aim to reveal the mechanisms behind these changes and their consequences for ecological processes (Shipley 2010; Culp et al. 2011). The approach builds on a highly integrative vision of the ecosystem. It considers simultaneously the ability of an organism to survive and reproduce in an environment, its interactions with other organisms, and its contribution to ecosystem functions (Green, Bohannan & Whitaker 2008). The concept transcends the notion of species, making trait-based studies more generalizable than taxonomic studies by providing a common currency to compare similar communities from different regions or environments with few species in common (McGill et al. 2006).

The description of ecological communities using functional traits is based on two hypotheses based respectively on the Grinnellian and Eltonian dimensions of the niche (Chase & Leibold 2003). First, the abiotic and biotic dimensions of the ecosystem act as filters selecting organisms that have traits allowing them to survive and reproduce (Keddy 1992). Second, organisms sharing the same traits have a

similar effect on ecosystem processes (Chapin et al. 2000). So far, the approach has been restricted mainly to plants (e.g. Cornelissen et al. 2003; Garnier & Navas 2012; Reich 2014), but functional diversity of ecosystems exists at multiple trophic levels and increasing our knowledge of functional traits of animals, bacteria and fungi is a priority (Duffy et al. 2007; de Bello et al. 2010; Lavorel et al. 2013).

The response trait approach is based on the hypothesis that the environment (landscape, abiotic conditions and biotic interactions) acts as a filter selecting individuals based on their traits (Diamond 1975; Southwood 1977; Keddy 1992) (Figure 1.1). Species with the right traits in a given situation will be more likely to increase their population size through higher performance (growth, survival, fecundity) (McGill et al. 2006) and immigration rate (Pulliam 2000). Response traits are used as proxies for performance (Violle et al. 2007) as performance can rarely be measured directly (McGill et al. 2006). As links are indirect, measured response traits should be related to environmental filters (e.g. humidity level, available food) to diminish the risk of spurious interpretation. If interactions between traits and environmental factors are well understood, it is expected that species sharing particular traits will react similarly even in different geographical regions, thus reveling ecological mechanisms involved in community assembly (Shipley, Vile & Garnier 2006; Shipley 2010; Laughlin 2014; Cadotte et al. 2015).

Effect traits determine the impact of an organism on ecosystem processes (Díaz & Cabido 2001). Ecological theory has argued that communities composed of species with high dissimilarity between their effect trait value could act complementarily through niche separation and facilitation (Loreau & Hector 2001). It means that a set of functionally different organisms can have a higher efficiency to accomplish a task (e.g. pollination, decomposition) than expect based on their individual efficiency (Loreau et al. 2001). Several experiments have shown this complementarity effect with plants, bacteria and invertebrates (Heemsbergen et al. 2004; Cadotte, Cardinale

& Oakley 2008; De Oliveira, Haettenschwiler & Handa 2010; Gravel et al. 2011; Coulis et al. 2015). Effect traits can also be used to evaluate the efficiency of different organisms to accomplish a task. For example, hairiest pollinators are expected to be better pollinators as they can transport a larger amount of pollen (Stavert et al. 2016).

Arthropods are a key element of terrestrial ecosystems because of their high diversity, abundance, ubiquity and their role in many important ecological processes including decomposition (Kočárek 2003; Handa et al. 2014) and pollination (Aguilar et al. 2006). They form the most diverse phylum of organisms with more than 1.2 million species described worldwide and probably as many undescribed (Grimaldi & Engel 2005). The functional trait approach is therefore particularly suitable, allowing to infer both abiotic (Kearney et al. 2010) and biotic niches (Eklöf et al. 2013) where the autoecology of species is poorly known (Langlands et al. 2011). Collecting such data is time consuming, expensive, and for rare species, practically impossible. Still, the potential use of functional traits to predict the ecological impact and the niche of arthropods remains largely unexplored. Also, few papers summarize the particularities of arthropods and how functional traits should be implemented in entomological studies (but see Pey et al. 2014b; Fountain-Jones, Baker & Jordan 2015; Moretti et al. 2016).

Our objective in this paper is to determine how the functional trait approach was integrated so far with terrestrial arthropods, and to propose solutions to improve the outcomes of future research on the subject. To do this, we reviewed the literature on the use of a functional trait approach with arthropods 1) to determine if postulated hypotheses permit to identify involved ecological mechanisms, and 2) to compile all the functional traits of terrestrial arthropods used in the published literature using the functional approach. The review highlights that the approach is often used in the absence of clearly postulated hypothesis which limits generalizations and the ability to identify ecological mechanisms. We also observed that studied traits are often

weakly related to studied functions, and cannot be generalized through taxa. To palliate these problems, we propose a step-by-step protocol to postulate clear hypothesis before selecting traits to studies and integrate more generalizable traits. We underline some important aspects of arthropods that may impede the integration of functional traits if not handled correctly, such as their high diversity, sex dimorphism and the difference between larval and adult stages. Finally, we propose a research agenda for the development and application of the proposed research approach.

1.2 Inconsistent use of arthropod functional traits in the literature

The literature review was done by searching published studies on the Web of Science and Google Scholar with the criteria "traits" + "function*" + all principal classes and orders of terrestrial arthropods (e.g. "arthropods", "insects", "spiders", "beetles", etc.). Citations were also tracked across papers. Only papers that were explicitly traits oriented were retained; i.e. papers that used arthropod functional traits to study the response to a perturbation or to an environmental filter (response traits) or their impact on ecosystem processes (effect traits). We deliberately concentrated our review on studies referring to the functional trait approach and therefore ignored other studies focusing on some aspects of organisms, such as morphology, but that are not relating them to their performance or ecosystem process. We did not include studies where the guild (or trophic level) was the only trait, as these typically describe a group of species rather than a functional attribute per se. We also rejected studies based exclusively on body size due to its commonness and the difficulty to formulate hypothesis relating this trait to a single environmental filter (see section 4). The literature review includes papers published before January 2017.

For all published papers that included response traits of arthropods, we evaluated if the elements present in the introduction, material and methods and supplementary materials permit to identify how the studied traits are mechanistically related to the subject of the study (explicit examples in Table A.1). It means that in a perfect scenario, we should be able to say; 'if [trait x] vary between communities, [process y] is involved in the structuring of the communities'. More precisely, we answered three questions (Figure 1.2). First, we checked whether environmental filters (abiotic, biotic and geographic) were clearly identified (Bremner 2008). To assess this aspect, we verified if environmental gradients expected to vary, and thus act as filters, were presented. Identified filters across studies were diverse and included humidity level, temperature, available food, diversity of predators, landscape fragmentation, etc. Cases where filters were clearly identified generally had a sentence in the form of 'We hypothesized a direct effect of [filter x] on [organism y] communities'. Other accepted forms were '[Perturbation z] is known to influence [filter x]'. Cases where the perturbation was related to the communities without identifying any clear filters (e.g. 'Land use will impact the community structure of [organism y]') were rejected. When a gradient was identified, but that this gradient did not permit to identify the filtering mechanism involved, the filter was considered as unidentified. For example, it will happen if a gradient of floristic composition is identified without further precision to determine if it affects vegetation structure, diversity of available food, microclimate, etc.

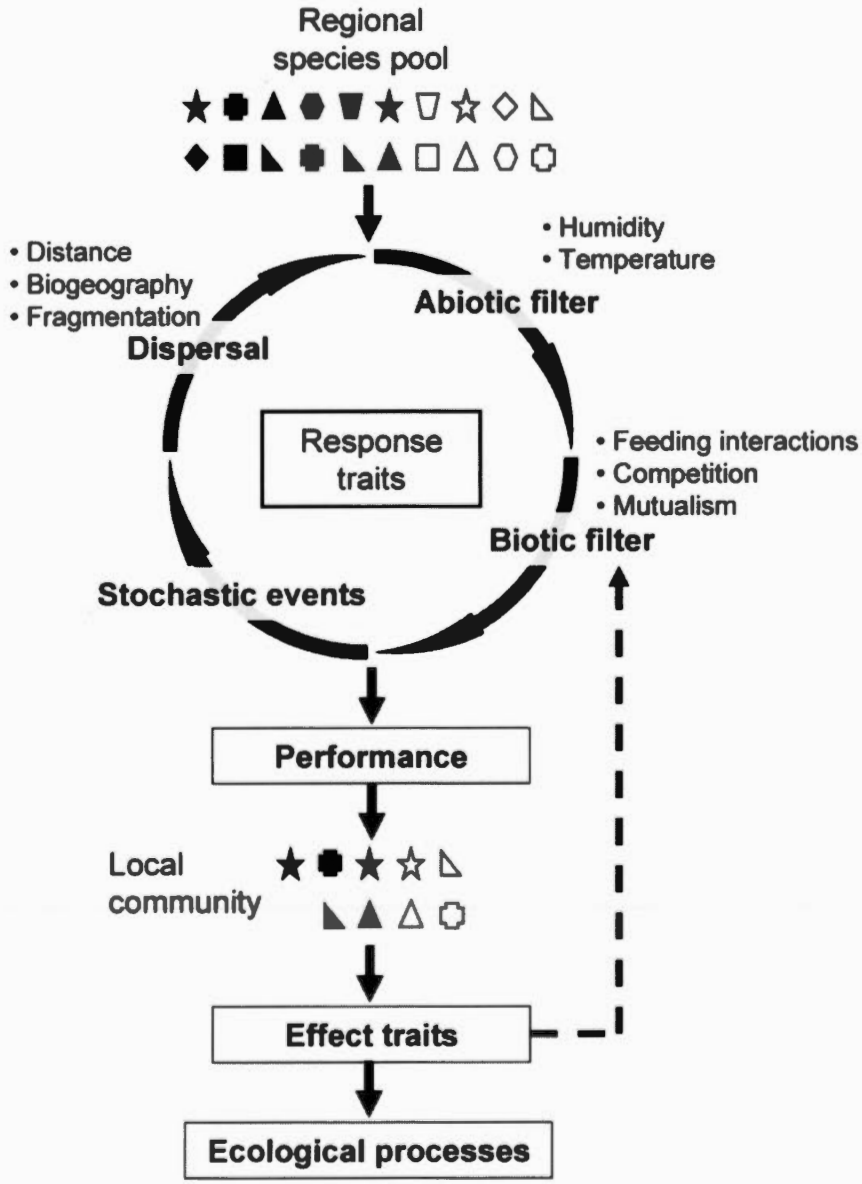

Figure 1.1 Hypothesized processes leading to a local species and trait assemblage from a regional pool. The regional species pool is first determined by evolution, biogeography and immigration/emigration with other regions. To establish themselves in the local community, species need to go through three filters acting simultaneously (represented as a cycling process with examples of limiting factors) selecting species based on their response traits. Performance represents growth rate, survival rate and fecundity. A feedback loop is expected between effect traits and the biotic filter (represented as a dashed line).

Secondly, we evaluated whether a clear hypothesis linking environmental filters to organismal functions was postulated (Naeem & Wright 2003). Functions were diverse and included dispersal ability, feeding interactions, thermal tolerance, fecundity, etc. (Table A.2). For this aspect, we looked for sentences in the form 'We hypothesized that [filter x] will influence the [function y]'. We also considered this aspect fulfilled in sentences such as '[Filter x] can have a negative/positive impact on species with a low/ high ability in [function y]'. It was considered as unfulfilled if the function was directly related to the perturbation, but the filters were not clearly identified.

Finally, we evaluated if the selection of all traits was explicitly justified by linking them to organismal functions and performance (Luck et al. 2012). We did not evaluate if the traits were well selected, but only if they were adequately justified. When adequately justified, the information was often shown in a table with a column 'Traits' and a column 'Role' or 'Hypothesized mechanism'. Alternatively, it was shown in the text as a sentence of the form '[Trait x] is related to the ability of the organism to [function y]'. Cases where justifications were considered as vague and thus unfulfilled were examples such as 'These traits are known to impact organism performance' or '[Trait x] is related to [function y]' without providing any reference. Only references explicitly demonstrating the mechanistic link between the trait and the function were accepted.

For studies using effect traits of arthropods, we evaluated two questions (Figure 1.2). First, we checked if the studied taxa were clearly related to the ecological process. This will generally appears in a sentence of the form '[Taxon x] is known to play a role in [ecological process y]'. We also accepted cases where the 'taxon x' was replaced by 'guild x' when the taxon was clearly related to this guild.

Secondly, we checked if the hypothesis relating selected traits and the ecological process were formulated. Justification of effect traits can be at two levels. They can

represent traits contributing to the functional dissimilarity and thus that are susceptible to create synergetic effect when combined (e.g. pollinators with different phenology can provide services throughout the growing seasons) or they can be used to compare the efficiency of different organisms. Otherwise, this aspect was evaluated as for the response traits.

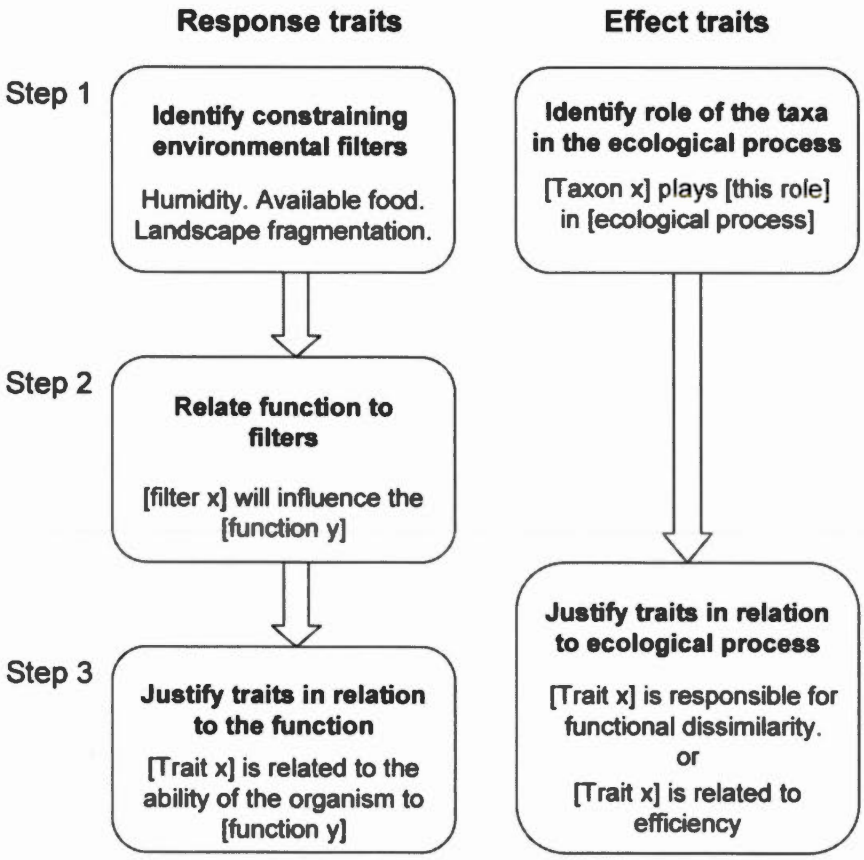

Figure 1.2 Schematized representation of a step-by-step protocol to postulate clear hypotheses in response and effect trait studies of arthropods.

Our review criteria yielded a total of 116 published studies (Annexe A); the earliest in 1996 (Castella & Speight 1996), but over three quarters of them (87) were published

since 2010. Studies on effect traits were underrepresented in the literature with only twelve published studies found. However, it is noteworthy that traits are often considered in the study of some ecological process and particularly for pollination, but without using a functional trait approach (Stang, Klinkhamer & van der Meijden 2006; Ibanez 2012). We excluded roughly one fifth of these studies (n = 18) from the reviewed response trait studies (n = 103) as they dealt with broader questions regarding conservation (e.g. Kotiaho et al. 2005) or evolutionary processes (e.g. Blaimer et al. 2015), for which it was impossible to answer our questions regarding trait selection and associated hypotheses.

Our analysis of whether studies were clearly hypothesis-driven revealed that only 23 % of response trait studies (n = 85) clearly met all three criteria (i.e. identifying environmental filters and postulating hypotheses linking traits, organismal functions and filters). When each criterion was considered individually, 59 % of the papers clearly identified environmental filters, 38 % offered hypotheses linking traits to environmental filters and responding organismal functions, and 37 % provided a justification for selected traits (Figure 1.3). Effect trait studies (n = 12) showed a more consistent approach with ecological processes and hypotheses being clearly identified in 70 % of the cases.

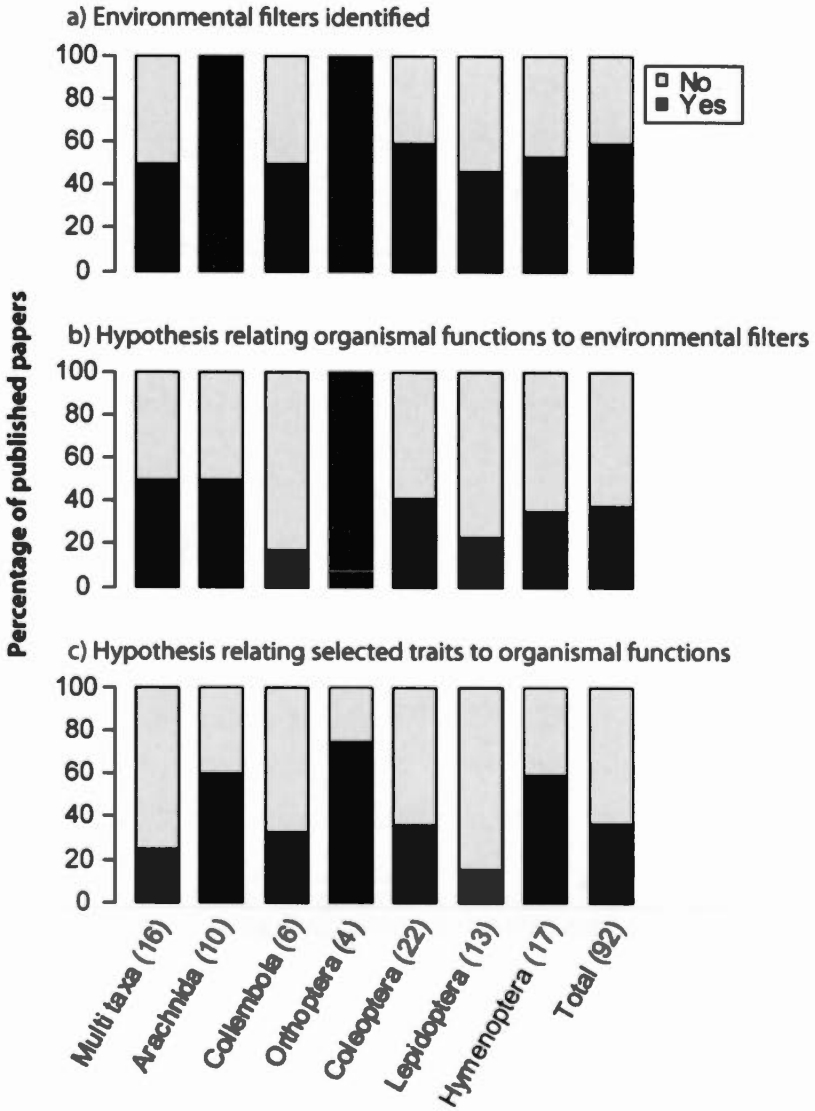

Figure 1.3 Percentage of published papers on response traits of terrestrial arthropods clearly identifying limiting environmental filters, and hypotheses linking traits, organismal functions and filters. Numbers in parentheses are the number of published papers per taxa.

Within the 116 surveyed studies, we distinguished 149 different response or effect traits associated to 50 different functions. They were summarized in relation to hypothesized dispersal, abiotic and biotic environmental filters or associated ecosystem processes (Table A.2). Some traits (33) were impossible to relate to a clear

function based on given information and were set apart in the category "function undescribed". Only 33 traits were repeated in at least three studies and with at least two taxa. We also classified each trait to the five categories (morphology, physiology, life history, behaviour and feeding) described by Moretti et al. (2016). Almost half of inventoried traits were morphological traits (71), while only ten physiological traits were found. The three other categories were represented with around 20 traits. Morphometric traits also represent 31 of the 33 traits that we were unable to assign to a clear function (Table A.2).

These results point towards the lack of a conceptual framework and collective approach to study the functional ecology of arthropods. Almost all studies were conducted independently with the purpose of increasing knowledge in particular research fields (e.g. land use, forest fire, ecology of a particular taxon), but not to establish common goals that would optimize the use of a trait-based approach. Considering the high diversity of arthropods, it is not surprising that disparities occur between studies; however, as measures of performance (growth rate, reproduction and survival) and ecological filters (dispersal, abiotic and biotic) remain the same between taxa, some generalities should emerge and understanding them would be useful.

The results of the literature review on functional traits of terrestrial arthropods revealed an inconsistency in the use of the functional approach. The interest behind the functional trait approach is to permit generalizations and help to develop a predictive ecology (Shipley, Vile & Garnier 2006). However, these objectives can only be reached if common goals are identified and that the science respect the right assumption (Shipley et al. 2016). While these assumptions were well identified in earlier studies (Reich, Walters & Ellsworth 1997; Lavorel & Garnier 2002; Naeem & Wright 2003; McGill et al. 2006; Petchey & Gaston 2006; Shipley et al. 2006), they seem to have been forgotten, even in plant ecology, with the increasing popularity of

the approach (Didham, Leather & Basset 2016; Shipley et al. 2016). With arthropods, over three quarters of response trait studies lack of clear hypotheses formulated regarding environmental filters, organismal functions and selected traits (Figure 1.3). This aspect can be easily resolved by going back to the basis and by postulating hypothesis allowing to identify involved ecological mechanisms (Figure 1.2).

The literature review also revealed an over representation of morphological traits, and that few traits are replicated across studies and taxa (Table A.2). Morphological traits are interesting as they are easy to measure, and can be measured on a high number of specimens and species. However, they do not always represent functionally important traits and should be used with caution (Didham, Leather & Basset 2016; Shipley et al. 2016). Furthermore, often, they cannot be generalized as they are associated with different functions across taxa. For example, length of the front legs of ground beetles can be associated with running speed (Forsythe 1983) while the same trait is related to prey type in orb-weaver spiders (Olive 1980) and to catching distance of prey in mantis (Michaels, Prindle & Turvey 1985). A functional trait approach needs to rely on functionally meaningful (i.e. related to fitness) and generalizable traits (Moretti et al. 2016; Shipley et al. 2016).

The problem relates to trait selection is more complex as it can only be resolved on the long term through experimentation and agreements between researchers. Nevertheless, this aspect should not be neglected in the short term as the relevance of any functional trait study is highly influenced by the selection of appropriate traits (Naeem & Wright 2003; Bartomeus et al. 2016). A first important step was made by the publication of a list of core traits with standardized protocol to measure them (Moretti et al. 2016). We encourage basing future studies on this list as much as possible, however, this list is not exhaustive and other traits are expected to be required in some circumstances. An important missing part is a list of traits determining interspecific interactions, i.e. traits of an organism that can be related to

the traits of a second organism to determine if they interact together. In the next section we demonstrate that this aspect can play an important role in different aspects of arthropods functional ecology from response to ecological processes.

1.3 Traits-matching

The functional trait approach could be highly interesting to determine the structure of ecological networks (Reiss et al. 2009; Morales-Castilla et al. 2015; Bartomeus et al. 2016; Gravel, Albouy & Thuiller 2016). In turn, the structure of ecological networks is seen as important component determining species distribution (Araújo & Rozenfeld 2014) and ecosystem processes (Loreau 2010). Traits relate to interactions can be used in a one-dimensional way (i.e. considering only the consumer point of view), or in a bi-dimensional way through trait-matching (i.e. by considering traits of both interacting organisms). In theory, trait-matching can be applied to any kind of species interaction (Morales-Castilla et al. 2015), however, it was poorly studied otherwise than for feeding and mutualistic interactions. In these cases, foraging traits of the consumers (e.g. body size, strength, length of the tongue) can be matched to vulnerability/ palatability traits of the resource (e.g. body size, toughness, depth of the corolla) to determine the probability of interactions between two organisms. An interesting aspect of trait-matching is that the same traits can be used to answer questions related to response (Le Provost et al. 2017) and effect traits (Deraison et al. 2015).

Trait-matching can help to identify how complex filters such as change in plant community structure affect arthropods community. Change in plant community structure is often proposed as an ecological filter affecting arthropods communities (e.g. Frenette-Dussault, Shipley & Hingrat 2013; Bargmann et al. 2016), but

identifying the right involved aspect can be tricky as it impacts several filters simultaneously. Identifying traits of plants affecting the filters and traits of arthropods affected by the filter could help distinguish the importance of each component. For example, the biting force of grasshoppers was shown to be related to the toughness of leaves of consumed plants (Ibanez et al. 2013; Deraison et al. 2015), and in turn, the toughness of leaves in a plant community is correlated to the biting force of grasshopper community (Le Provost et al. 2017). We are not aware of other studies using trait-matching to explain community structure, but some hypothesis can be postulated. As leaf area and root length of plants have an impact on soil humidity (Gross et al. 2008), we can hypothesize that variation in these traits in plant communities will have an impact on the desiccation resistance of soil arthropod communities. The interest of such hypothesis is that it permits a direct link between plants and arthropods, and is less tautological than hypothesizing that moisture variation impact the desiccation resistance of arthropods.

Trait-matching can also be used in effect trait studies by giving information on the efficiency of an organism in a particular task (Schleuning, Fruend & Garcia 2015). This aspect was principally studied with pollinators, and more precisely, the matching the proboscis length of the pollinator and the depth of the corolla of the flower (Inouye 1980; Kunte 2007; Ibanez 2012). This trait-match is a good predictor of species interactions (Ibanez 2012) and of the handling time; thus of the number of visited flowers and pollination efficiency (Inouye 1980; Herrera 1989). It was also suggested that the location of the hairs on the body of the pollinator can be matched to the morphology of the flower to determine the efficiency to pollinate a flower (Stavert et al. 2016). A rare example with herbivores shown that biting force of grasshoppers determine their feeding niche and their impact on plant biomass (Deraison et al. 2015).

Works on the decomposition of leaves demonstrate that increasing the functional diversity of both decomposers and leaves litter traits increase the decomposition rate (Coulis et al. 2015). This could be related to resource preference shown by decomposers (David 2014) and by a matching of their traits with physical and chemical traits of leaf litter affecting their assimilation efficiency. Traits of the faeces of decomposers (e.g. C:N ratio, fragmentation of plant material) can also influence microbe activity and be related to the decomposition rate (Hedde et al. 2007). As the traits of the faeces are influenced by the traits of the decomposers (Köhler & Alberti 1990; Frouz & Šimek 2009) and the traits of the leaves (Coulis et al. 2016), we can hypothesize that trait-matching could help to better understand the impact of functional diversity on decomposition rate. However, we need more experimentation on this aspect to understand the impact of functional diversity on decomposition rate.

1.4 Particularities of arthropods

1.4.1 Treating several taxa simultaneously

Arthropods are highly diverse in species, shape and morphological structure which complicate their study as a whole in functional trait studies. Typically, studies incorporating several taxa tend to include only very general traits (e.g. body size, dispersal ability, phenology) (e.g. Moretti & Legg 2009; Hedde et al. 2013). However, understanding community structure and ecosystem processes are unlikely with singular very general traits (such as body size) (Enquist et al. 2015). In particular, body size is widely studied and has allowed summarizing complex ecological networks (Gravel et al. 2013). However, its predictive ability varies enormously across ecosystems, particularly between aquatic and terrestrial ones (Riede et al. 2011). Body size is also central to the metabolic theory of ecology

(Brown et al. 2004), but even then, its predictive power is limited to 2-20 % of observed variation in metabolic function for species in a 10-fold size range (Tilman et al. 2004), a scale corresponding to that typically observed in arthropod communities. A contrasting approach for studies across taxa has been to use a different set of traits for each taxon (e.g. Barbaro & van Halder 2009; Aubin et al. 2013). This approach allowed investigations across trophic levels, however, by separating taxa sharing similar niches in the analyses diminishes the power of inference. This challenge points to the importance of establishing standard traits (e.g. biting force, dispersal distance, water loss rate etc.) to increase our capacity to infer across taxa and processes. Another aspect to consider is that different strategies can evolve to resolve the same problem; thus different trait value can result in the same niche (Young, Haselkorn & Badyaev 2007). For example, two different strategies can be used to eat a snail: crushing the shell with strong mouthparts or attacking through the aperture with long appendices (Nyffeler & Symondson 2001). Thus, the traits should be selected to reflect the outcome (in this case, the feeding niche) of the trait instead than the trait per se. For example, traits as biting force or size of the mouthparts are both relate to the feeding strategy. However the biting force probably has the same outcome for the insect and the arachnid, it is just calculated differently (van der Meijden et al. 2012; Moretti et al. 2016). On the other hand, it is unclear if the length of the mandibles can be compared to the length of the chelicerae.

1.4.2 Larvae vs. adults

In many arthropods taxa (Odonata, Coleoptera, Lepidoptera, some Acari, etc.), immature stages are morphologically and/or ecologically drastically different from adults, and thus face different constraints. In some cases, response traits of the immature could be more important than those of the adults, particularly for capital

breeders (Teder, Tammaru & Esperk 2008), i.e. species for which important traits such as size and fecundity are determined by the resources they accumulate during the immature stages (Tammaru & Haukioja 1996). It is also true for effect traits of defoliators, as immature (e.g. caterpillars) generally cause the most important damages.

Including traits from a stage that is not associated with an environmental filter or active in the studied ecological process will not only be meaningless, but may lead to misinterpretation. The way to treat immature stages will vary depending on the subject and the taxa studied. For ametabolous taxa, the value of the traits of the immature represents an intraspecific variation (Violle et al. 2012). The problem is different for holometabolous taxa, as immature stages can be in a different traits space than the adults. When it is the case, we suggest treating both stages separately to allow considering intraspecific variation caused by stage differences. Another significant advantage is that it would allow integrating larvae in the analyses even if the exact species is impossible to determine.

1.4.3 Females vs. males

Sex dimorphism is a particularity of animals that can pose a problem while measuring traits. Female arthropods are generally larger than males, and sexual selection affects principally males so that they often present hypertrophied mandibles or other particularities. In some cases, the difference can be tremendous with males and females looking like two different species. In such situations, using the mean value will yield a trait value representing neither sex, while the median gives the value of the most often caught sex. As for larvae, females and males should be treated distinctly when differences are major.

1.4.4 Ecological preferences and feeding guilds

Confusion arises in many functional trait studies with the use of 'habitat preference' or 'guild' (predator, herbivore, granivore, etc.) as functional traits. Based on a strict definition, habitat preference is not a trait as external variables are required to define them (Violle et al. 2007), but falls under the broader category of "ecological preference" (Pey et al. 2014b). Feeding guilds are more problematic but are generally considered as a trait (Van den Brink et al. 2011; Moretti et al. 2016). In a way, guilds can be compared to the growth forms of plants; i.e. representing an important niche separation that cannot be ignored, but of poor predictive power (Lavorel et al. 1997; Petchey & Gaston 2006; Wright et al. 2006; Frimpong & Angermeier 2010; Fountain-Jones, Baker & Jordan 2015). Guilds reveal little information on the mechanisms involved in community structuring and can hardly be related to performance (Blaum et al. 2011). For example, determining that herbivores are disadvantaged by a perturbation does not reveal the underlying mechanism (e.g. decreasing resources, increasing competition, increasing predation, decrease in the quality of abiotic conditions or a sampling effect). For this reason, we recommend considering guilds as a high-level functional group used to split analyses, but not to serve explicitly as response or effect traits.

1.5 Towards a trait-based approach for terrestrial arthropods

1.5.1 Determining a standard set of traits to study

Establishing a standard set of traits to document is necessary to facilitate generalizations across studies. These core traits should be related to the dispersal/ colonization ability, tolerance to abiotic factors and feeding interactions. A first list of

traits with standardized protocol for their measurement was recently published (Moretti et al. 2016) which we encourage following when possible. The main missing aspect now is a list of traits related to species interactions. Principally, we need traits relate to other interactions than feeding which are almost completely missing. Also, it was shown that it was possible to predict realized interactions of predators based on traits only, however unrealized interactions were predictable only based on the phylogeny (see Chapiter 2). This demonstrates that we miss valuable information by lacking a better knowledge of traits impeding interactions.

Another aspect that was neglected is to conduct experimentation clearly demonstrating the link between traits of arthropods and their performance (Moles et al. 2011; Violle et al. 2014; Asner et al. 2016). So far, these links are merely hypothetical and tested only at local scale and are thus subject to local-dependent effect that can impede robustness, generalizations and predictive abilities (Violle et al. 2014). This aspect can be improved by analyzing large scale dataset to determine how functional traits respond to environmental changes (Violle et al. 2014). However, large datasets of traits are required to achieve these goals (Violle et al. 2014).

1.5.2 Data gathering and repositories

Development of open access databases are required to synthesize as much data as possible and allow more complete and generalizable studies. The only open databases for terrestrial arthropods that we know of are the BETSI database for soil invertebrates (Pey et al. 2014a) and Carabids.org for the ground beetles of the Palaearctic region (Homburg et al. 2014). Databases are essential to synthesize the high amount of information available in specialized literature (Luck et al. 2012; Pey

et al. 2014b). For example, information on the metabolic rate of many species has been published (e.g. Reinhold 1999). Data gathering requires the establishment of a common language to describe traits and ancillary data to prevent misinterpretation of available data (Pey et al. 2014a; Shipley et al. 2016). A part of the work was done for soil invertebrates (Pey et al. 2014a), but it needs to be generalized, ideally for all animals.

One problem in the philosophy behind open databases, which could impede their development, is that they are highly profitable to users, but not profitable to contributors. This problem could be resolved by encouraging data citations and other measures for the recognition of contributions (Baird et al. 2011; Poisot, Mounce & Gravel 2013). However, such databases are almost useless if traits are not defined properly (Baird, Rubach & Van den Brink 2008) and thus a complementary beneficial effect of open databases is to promote the use of standardized measures of traits (Homburg et al. 2014).

1.6 Conclusion

The use of functional traits to study plant community structure and dynamics is highly profitable for community ecologists, as well as for applied ecology. Studies of arthropod functional traits should be as profitable. Nevertheless, we must keep in mind that a trait based approach is a simplification of a species based approach. The strength is in the capacity to generalize and offer clear mechanisms, thus emphasizing the importance to apply a hypothesis based framework for studies. As active heterotrophs, the reality of arthropods is tremendously different from the reality of sessile autotrophs as plants. This reality needs to be considered by giving a higher importance to the traits related to their interspecific interactions as well as their

dispersal ability. Identifying the right set of traits to study arthropods will be a long challenge because of their diversity and the lack of data for many taxa. However, with the development of good traits and databases to share this information, it could become a powerful tool in the future.

CHAPITRE 2

TRAIT-MATCHING AND PHYLOGENY AS PREDICTORS OF PREDATOR-PREY INTERACTIONS INVOLVING GROUND BEETLES

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2.1 Abstract

With multiple global change drivers modifying species assemblages within ecosystems, our success in predicting ecosystem level consequences of these new communities will depend on our ability to understand interactions between species. Current food web theory considers interactions between numerous species simultaneously, but descriptive models are unable to predict interactions between newly co-occurring species. Incorporating proxies such as functional traits and phylogeny into models could help infer predator/ prey interactions. Here we used trait-matching between predator foraging traits and prey vulnerability traits, along with phylogeny, to infer predatory interactions using ground beetles as model organisms. A feeding experiment was conducted involving 20 ground beetle and 115 prey species to determine which pair of species did or did not interact. Eight predator and four prey traits were measured directly on specimens. Then, using a statistical approach based on the matching-centrality formalism, we evaluated 511 predictive models that tested different combinations of all predator and prey traits, and phylogenetic information. The most parsimonious model accurately predicted 81 % of the observed realized and unrealized interactions, using phylogenetic information and the trait-matches predator/ prey body size ratio and predator mandibular strength/ prey cuticular toughness. The best trait-based models predicted correctly >80 % of realized interactions, but were unable to predict unrealized interactions. Adding a phylogenetic term representing the evolutionary distance within each trophic level increased the ability to predict unrealized interactions on average by 24 %. The matching of predator mandibular strength and prey cuticular toughness demonstrated a better predictive power than the commonly used predator/ prey size ratio. Our novel model combining both traits and phylogeny to accurately predict predator/ prey interactions extends beyond existing descriptive approaches and could represent a

valuable tool to predict consumer/ resource interactions of newly introduced species and to resolve cryptic food webs.

2.2 Introduction

Predicting the dynamics of novel communities arising with global change will depend on our ability to understand interactions between species (Van der Putten, Macel & Visser 2010). Current food web theory considers simultaneous interactions between a high number of species and is useful to anticipate the consequences of species extinction on the structure of food webs (Dunne, Williams & Martinez 2002). Its predictive ability is however limited to known interacting species and is thus unable to predict interactions between newly co-occurring species resulting from a recent invasion or a range shift (Gravel et al. 2013). A further problem is that food web models are limited by the documentation of interactions. It is not feasible to document all potential interactions between species of a region with traditional techniques (direct observation, DNA analysis of gut content, etc.), making it important to develop inference tools (Morales-Castilla et al. 2015).

Recent descriptive models of food web structure rely on two important sources of information; functional traits (Petchey et al. 2008; Allesina 2011) and phylogeny (Cattin et al. 2004; Bersier & Kehrli 2008). Functional traits represent any characteristics measurable at the individual level influencing the fitness of an organism (Violle et al. 2007) and could be instrumental to determine foraging ability of a consumer and the vulnerability of the resource. Previous studies demonstrate that most ecological networks can be represented in a three to five dimensional space, presumably related to functional traits (Eklöf et al. 2013). Phylogeny is used as a proxy of similarity in trait values between related groups of species (Webb et al.

2002) and accordingly indicates an evolutionary based conservatism in interactions of close relatives (Bersier & Kehrli 2008). This aspect could be particularly important for traits that are hard to measure, such as chemical defense of prey (Eisner, Eisner & Siegler 2005) or digestive enzymes of predators (Feyereisen 1999).

Although mixing both traits and phylogeny could be efficient to predict ecological interactions (Morales-Castilla et al. 2015), food web models including them are descriptive only (Rezende et al. 2009; Rohr et al. 2010; Rafferty & Ives 2013; Krasnov et al. 2016). The few existing predictive models are still based uniquely on trait-matching (Gravel et al. 2013; Rohr et al. 2016). The trait-matching approach takes into account the probability of interactions between the traits of the consumer and the traits of the resource (Rohr & Bascompte 2014; Gravel, Albouy & Thuiller 2016a). An example of trait-matching would be the matching of pollinator tongue length with flower traits such as corolla tube depth (Ibanez 2012). Similarly, traits of marine mammal predators such as swimming speed and muscle lipid content can be matched to prey traits such as lipid and caloric content (Spitz, Ridoux & Brind'Amour 2014).

The trait-matching approach has been extended through the matching-centrality formalism, which considers simultaneously the matching and the centrality components of a network and has the added advantage of being able to predict unobserved, but existing links between rare or newly co-occurring species (Rohr et al. 2016). The matching component quantifies the compatibility between the foraging traits of the consumer and the vulnerability traits of the resource. The centrality component determines the specificity/ generality of a species; in other words, species sharing similar traits are expected to realize a similar number of interactions (Rohr & Bascompte 2014). Each species (consumer and resource) is characterized by a set of matching traits and centrality traits; these could be evaluated as latent variables or directly using measured traits (e.g. body size, tongue length, nectar holder depth). The

phylogenetic position of a species in a community could be used as an intermediate since it is essentially a latent variable aimed to represent unmeasured functional traits (Cadotte et al. 2009). It provides an elegant solution to circumvent problems related to the measurement of some traits, but the drawback is that one does not acquire insight into possible mechanisms as when measuring true functional traits.

In the specific case of predator/ prey interactions in terrestrial environments, the use of trait-matches to predict interactions has been limited to the size ratio of predator and prey through the matching-centrality formalism (Gravel et al. 2013). Other known important traits of predators such as biting force (Wheater & Evans 1989; Christiansen & Wroe 2007) and handling ability (Brodie & Formanowicz 1983; Cunha & Planas 1999) have yet to be matched to relevant prey traits. For instance, the cuticular toughness of prey can act as an armor protecting them from weaker predators (Broeckhoven, Diedericks & Mouton 2015). Such matching could create a shift in the predator/ prey size ratio relationship such that the predator could interact with larger soft prey and smaller hard prey (Enders 1975). Including these traits could help to refine trait-matching models, but so far, neither their descriptive nor they predictive ability were quantified for any system.

Our objective was to develop a predictive model to infer predator/ prey interactions using ground beetles (Coleoptera: Carabidae) as model organisms. We used functional traits as the main predictors of interactions, based on the matching-centrality formalism, and we complemented our analysis with phylogenetic information to represent traits that were not documented or that were hard to measure. Our working hypothesis was that both traits and phylogeny would explain most of the observed feeding interactions. Our predictions were that i) the most important ground beetle traits would be body size, mandibular gape and mandibular strength (Evans & Forsythe 1985; Wheater & Evans 1989; Cohen et al. 1993) combined respectively to the prey traits body size, body width and cuticular toughness, and ii) ground beetles

belonging to the same clade would be more likely to share prey than distantly related ones. We tested these predictions with a feeding experiment to determine prey with which different species of ground beetles did or did not successfully interact. Then, we predicted the feeding interactions of ground beetles based on the matching-centrality formalism.

2.3 Material and methods

Collection of specimens

Ground beetles and their prey were collected at several sites and in various habitat types in southern Quebec, Canada, to maximize phylogenetic and morphological diversity. Overall, we collected specimens of 20 species of ground beetles representing 13 genera, nine tribes and four sub-families (Table 2.1 and B.1) and a total of 115 prey species of arthropods (woodlice, millipedes, caterpillars, spiders, etc), earthworms, mollusks and land planarians (Table B.2). These included all life stages from eggs to dead specimens. Prey were identified to the lowest taxonomic level we were able to reach, or were classified as morphospecies (hereafter referred to as species), when species level identification was impossible. We kept at least one specimen of each species in 70 % alcohol when possible (i.e. when we had more than one specimen on hand) to measure traits that could not be assessed on live specimens. Likewise, all ground beetle predators were preserved in 70 % alcohol.

Table 2.1 List of ground beetle species studied and summary of the realized (+) and unrealized (-) interactions observed in the feeding experiment, derived from the literature (only realized) (Lit.) (Larochelle & Larivière 2003), or from forbidden links (FL), and the total of interactions included in the analysis.

Subfamily Tribe	Species	Observed interactions +	-	Lit.	FL	Total
Carabinae						
Carabini	*Carabus nemoralis* Müller	7	12	12	0	31
Harpalinae						
Harpalini	*Anisodactylus harrisii* LeConte†	14	4	0	1	19
	Harpalus providens Casey†	5	6	11	1	23
Perigonini	*Perigona nigriceps* (Dejean)†	17	10	0	16	43
Platynini	*Agonum retractum* LeConte†	7	4	0	6	17
	Platynus opaculus (LeConte)†	6	3	0	1	10
	Platynus tenuicollis (LeConte)†	24	17	0	1	42
Pterostichini	*Myas cyanescens* Dejean	0	14	1	1	16
	Pterostichus caudicalis Say	12	2	0	1	15
	Pterostichus coracinus (Newman)†	40	31	12	3	86
	Pterostichus diligendus (Chaudoir)†	17	17	11	1	46
	Pterostichus lachrymosus Newman	6	5	11	1	23
	Pterostichus mutus Say†	7	6	11	1	25
	Pterostichus rostratus (Newman)†	27	16	8	1	52
	Pterostichus tristis (Dejean)†	40	27	11	1	79
Sphodrini	*Synuchus impunctatus* (Say)	3	1	0	1	5
Nebriinae						
Nebriini	*Nebria lacustris* Casey†	17	16	0	1	34
Notiophilini	*Notiophilus aeneus* (Herbst)	5	2	0	10	17
Trechinae						
Bembidiini	*Bembidion chalceum* Dejean†	11	7	0	10	28
	Elaphropus anceps (LeConte)†	4	6	0	16	26
	Total	269	206	88	74	637

† Species for which necrophagous habits were observed during the feeding experiment.

Feeding experiment

We conducted a total of 475 pairwise feeding experiments in the laboratory in a regulated environment at 24°C, 70 % humidity and a day/ night cycle of 16/ 8 hours. Given the major effort to collect organisms (e.g. once or twice a week for two months), identify them and keep them alive prior to the experiment, pairwise tests were generally not replicated, and not every possible interaction was tested. Nonetheless, interactions were chosen to maximize the variation in traits and phylogenetic diversity of prey for each ground beetle species (Annexe C). Ground beetles were kept separately in plastic containers of 11 × 11 × 4.5 cm lined with a moistened filter paper at the bottom. Filter paper was moistened daily and changed twice a week.

Ground beetles were starved for 24 h prior to the feeding experiment, after which they were provided with one prey at a time. Prey consumption was recorded after 24 and 48 h. A realized interaction was noted if the prey was killed and consumed at least partially. An unrealized interaction was recorded if the ground beetle did not kill the prey after 48 h. On two occasions, the ground beetle successfully killed the prey, but did not consume it; the interaction was considered as unrealized.

Functional traits

Ground beetle and matched prey traits were selected to represent hypothesized limitations in their potential interactions (Table 2.2). These limitations included 1) predator/ prey size ratio (measured as body length) which is a commonly used proxy for physical limitation of interactions (Cohen et al. 1993); 2) predator mandibular strength (estimated from allometries with head and mandibular size (Wheater & Evans 1989)) that was to match prey cuticular toughness (Wheater & Evans 1989;

Broeckhoven et al. 2015); 3) predator mandibular gape, which is related to handling ability and was to match prey body width (Evans & Forsythe 1985); and 4) predator eye size that was to match the speed of movement of prey (Bauer & Kredler 1993). We also included four predator traits associated to mandibular characteristics hypothesized to relate to prey handling (Evans & Forsythe 1985; Acorn & Ball 1991), but that were difficult to match to any prey traits. These were mandibular length, length of liquid absorption section, length of cutting section (terebra) and length of apical tooth. Body length instead of body mass was selected for practical reasons: it was impossible for us to weigh prey before offering them to predators, and metrics to estimate body mass were not available for many of our prey types. All measurements of ground beetle traits were made on alcohol-preserved specimens under a dissection microscope with a graduated eyepiece. Body length and width of prey were measured when possible on living specimens. Cuticular toughness of prey was measured on dead specimens with a Pesola® pressure set (Medio-Line) to which we added an entomological pin of 0.45 mm of diameter. All traits, except for cuticular toughness, were measured on every individual ground beetle and prey specimen. Cuticular toughness was measured on one to six specimens per species (depending on availability); a mean trait value per species was used for model construction. Further detail on the methodology used to measure traits can be found in Annexe C.

Phylogeny

The phylogenetic distance matrices of prey and ground beetle species were based on taxonomic level. For each of the 15 taxonomic levels (species to super-phylum), the distance was incremented by one so that it characterized only the topology of the tree. For morphospecies, the distance was assigned as the next taxonomic level; e.g. all Noctuidae sp. were considered as belonging to different sub-families. Principal coordinates analyses (PCoA) were performed on both ground beetle and prey distance

matrices to determine the position of each species in the phylogenetic space. The PCoA were performed on a δ transformed phylogenetic distance matrix to reduce the importance of superior taxonomic levels on the species scores permitting a finer resolution between lower taxa (orders, families, genera) (Pagel 1997). We selected the δ value for each group giving the best goodness-of-fit of the model with the hypothesized trait-matches predator size/ prey size, predator mandibular strength/ prey cuticular toughness and predator mandibular gape/ prey body width; it was set to three for ground beetles and six for prey. The phylogenetic score of all eggs, pupa and dead specimens of a particular prey species was set to the same value corresponding to 50 points over the previous stage group on both axes. By so doing, it was possible to correctly distinguish interactions of ground beetles with inactive stages of prey from interactions with active stages.

Statistical analysis

We recorded for each tested pair of species (i, j) if they interacted or not (noted L_{ij}). Realized interactions were coded as $L_{ij} = 1$ and unrealized interactions $L_{ij} = 0$. When development stages of a same species were highly different, they were included as two different species (e.g. immobile stages vs. mobile stages, larva and adult of holometabolous insects), each with their own trait values. Overall, the matrix included 151 prey types. We added 88 realized interactions reported in Larochelle and Larivière (2003); only interactions we could confirm from cited references were included (Table 2.1). For these 88 cases (representing 13 prey species), prey were attributed trait values of equivalent measured specimens. No unrealized interactions were included from the literature as these have been rarely documented. We also added 74 forbidden interactions (Morales-Castilla et al. 2015) between the smallest predators and larger prey, such as between the ground beetle *Elaphropus anceps*

(LeConte) (size = 2.1 mm) and the millipede *Narceus americanus* (de Beauvois) (size = 70 mm).

Table 2.2 Traits considered in the investigation of ground beetle/ prey interactions based on the matching-centrality formalism.

Traits	Function
Ground beetle traits	
Body length	Body length is used as a measure of body size. It is a commonly used proxy of physical and physiological constraints of interspecific interactions (Cohen et al. 1993).
Mandibular strength	Related to the ability to use strong and hardened food (Wheater and Evans 1989).
Mandibular gape	Determines the handling ability; i.e. the maximum size (width) of used prey (Evans and Forsythe 1985)
Eye size	Related to the visual acuity and the movement speed of used prey (Bauer and Kredler 1993)
Mandible length	Assumed to be related to prey handling
Terebra length (cutting edge of mandibles)	Longer for strict predators; shorter for omnivores (Evans and Forsythe 1985); assumed to be related to prey handling
Length of absorption section of mandibles	Longer on liquid feeders (Evans and Forsythe 1985); assumed to be related to prey handling
Length of apical tooth of mandibles	Handling ability; maintains the prey in place while slicing it with the terebra (Acorn and Ball 1991); assumed to be related to prey handling
Prey traits	
Body length	As for ground beetles
Cuticular toughness	Hard cuticle acts as an armor against predators (Broeckhoven et al. 2015)
Body width	Animals with thin body could be easier to handle by predators
Movement speed	Fast moving prey are more difficult to catch

Matching-centrality formalism

Interactions were analyzed following the matching-centrality formalism (Rohr et al. 2016). Each species was represented by a "matching" and a "centrality" component. The "matching" component represented the combined effect of predator (f_j) and prey (v_i) traits; i.e. how the traits interact. The "centrality" component represented the direct effect of the traits alone for predator and prey, i.e. accounts for their respective specificity/ generality relative to the number of associated prey or predators. The probability of interaction $P(L_{ij} = 1)$ based on a general linear model (GLM) follows a log-linear model of the form (Rohr et al. 2016):

$$\text{logit}(P(L_{ij}=1)) = -\lambda(v_i - f_j)^2 + \delta_i v_i^* + \delta_2 f_j^* \quad (1)$$

where λ, δ_1 and δ_2 are parameters describing the importance of the "matching" $(v_i - f_j)^2$ and of the "centrality" of prey (v_i^*) and predators (f_i^*). Ecologically, the v term represents the vulnerability of the prey, while the f term represents the foraging ability of the predator (Rohr & Bascompte 2014). Rohr et al. (2016) evaluated latent traits and related them after to observed traits, while here we considered them directly. We tested four hypothesized trait-matches that included predator body length/ prey body length, predator mandibular strength/ prey cuticular toughness, predator mandibular gape/ prey body width and predator eye size/ prey speed of movement. For unmatched predator traits (Table 2.2), only the centrality was accounted for. We also considered the phylogenetic position of a species (as determined by PCoA scores along the first two axes), which is equivalent to a latent trait representing the conservatism of interactions resulting from evolutionary processes (Bersier & Kehrli 2008; Morales-Castilla et al. 2015).

General Additive Models (GAM)

We used general additive models (GAM) which permit a higher flexibility than general linear models (GLM) (Wood 2006) to fit the matching-centrality formalism. GAMs are based on a smooth function determining the number of inflexion points in the curve of the model for each term. High smoothing can, however, force the curve to over-fit observed data such that missing data highly influence the shape of the curve and can make it ecologically meaningless (Wood 2006, p. 128). To prevent this problem, we tested separately each trait-match to find the lowest smoothing limit from which a smooth curve representing the hypothetical relationship was obtained (Annexe D).

We fitted the phylogenetic model as an interaction between the scores of the two PCoA axes of ground beetles and prey. This model thus explains the probability of a species to interact with another based only on its position in phylogenetic space. The new equation for the matching-centrality formalism, based on a GAM and including the phylogenetic component, is given as:

$$\mathrm{E}\left(P(L_{ij}=1)\right)=s_1\left(PCoA1_{fi},PCoA1_{vi}\right)+s_1\left(PCoA1_{fi},PCoA2_{vi}\right)+s_1\left(PCoA2_{fi},PCoA1_{vi}\right)+ s_1\left(PCoA2_{fi},PCoA2_{vi}\right)-\lambda\left(s_2(v_i-f_i)^2\right)+\delta_1 s_3\left(v_i^*\right)+\delta_2 s_4\left(f_i^*\right) \quad (2)$$

where s_x are smooth functions and $PCoAx_{fi}$ and $PCoAx_{vi}$ are respectively PCoA scores for predators and prey on axis x.

The over-fitting of the phylogenetic term by the GAM cannot be evaluated visually as for the trait-matches. Thus, we created a null model assuming a random phylogenetic relationship between ground beetles and prey species. In a first step, the phylogenetic scores of ground beetles and prey species were randomized. Then, we calculated the true skill statistic (TSS) of a model based on equation 2 including only the phylogenetic term. We varied the degrees of smoothing (s_1) from 10 to 30 with a step of two. These operations were performed with 500 iterations for each degree of

smoothing. We kept the upper degree of smoothing for which the mean TSS was within the range of the null models (information on TSS and null models provided below), i.e. the higher smoothing value for which a randomized phylogeny did not predict more interactions than chance alone. The degree of smoothing was fixed at 24. All smoothing was done using the "Thin Plate Regression Splines (TPRS) with shrinkage" approach (Wood 2006). The gamma term was set to 1.4 to prevent over-fitting (Kim & Gu 2004). All models were computed as a binomial regression using the function 'gam' in the R package '*mgcv*' (Wood 2015).

Goodness of fit

We wanted to determine the predictive ability of predator/ prey interactions of each trait-match, unmatched trait and the phylogenetic term, but also to determine which model had the best fit. The goodness-of-fit was defined based on four metrics: accuracy, sensitivity, specificity and true skill statistic (TSS) (Allouche, Tsoar & Kadmon 2006). Accuracy is the percentage of well-predicted realized and unrealized interactions; sensitivity is the percentage of well-predicted realized interactions and specificity is the percentage of well predicted unrealized interactions. All three measures have a value between 0 (absence of good prediction) and 1 (perfectly predicted). TSS represents correct predictions in relation to incorrect predictions and varies between -1 (incorrectly predicted) and 1 (perfectly predicted). The goodness-of-fit was computed for all possible combinations of the four trait-matches, four unmatched traits and the phylogenetic term (representing a total of 511 possible combinations of the nine terms - Table E.1).

For many prey species, we observed a wide range of trait values reflecting intraspecific variation. Given that predator/ prey interactions would be influenced by this variability, the probability of interaction was calculated for all potential

combinations of prey trait values considering a step of 0.5 mm for length and width, and a step of 2 g mm^{-2} for cuticular toughness. No variation was allowed for speed of movement. Predicted realized interactions between a ground beetle and a prey species were determined in two steps. First, the predicted probability of interaction needed to be ≥ 0.5 for at least one combination of the trait value of the prey. Second, the model needed to predict at least 25 % of realized interactions. This approach allowed us to eliminate cases where the ground beetle was predicted to interact only with individuals of the species with extreme trait values.

Null model

We tested the statistical significance by comparing the predictive ability of the models with two null models. The first null model hypothesized that interactions were distributed independently of traits, phylogeny or species. This scenario was computed by randomizing the interactions in the observed matrix between predators and prey. The second null model hypothesized that the level of specialization (number of interactions observed) was species-specific for ground beetles, but that traits and phylogeny were not involved. In this scenario, interactions of the observed matrix were randomized only between prey, so that each ground beetle species always had the same number of realized and unrealized interactions. Ten thousand iterations were run for both null models. We calculated accuracy, sensitivity, specificity and TSS for each randomized matrix. Significance of each aspect of the tested models (accuracy, sensitivity, specificity and TSS) was determined by calculating standardized effect size (SES) with the formula $SES = (I_{obs} - I_{sim})/\sigma_{sim}$ where I_{obs} is the observed value, and I_{sim} and σ_{sim} are respectively the mean and the standard deviation of the null model. The SES was calculated for both null models after verifying normality, and the mean value was used to test the significance (Veech

2012). We accepted that a SES>1.96 (P<0.05) indicated a better goodness-of-fit than the null models (Veech 2012).

The over-fitting of the phylogenetic term by the GAM could not be evaluated visually as for the trait-matches. Thus, we created a null model assuming a random phylogenetic relationship between ground beetles and prey species. In a first step, the phylogenetic scores of ground beetles and prey species were randomized. Then, we calculated the TSS of a model based on equation 2 including only the randomized phylogenetic term. We varied the degree of smoothing (s_1) from 10 to 30 with a step of two. These operations were performed with 500 iterations for each degree of smoothing. We kept the upper degree of smoothing for which the mean TSS was within the range of the null models, i.e. the higher smoothing value for which a randomized phylogeny did not predict more interactions than chance alone. The degree of smoothing was fixed at 24. All smoothing was done using the "Thin Plate Regression Splines (TPRS) with shrinkage" approach (Wood 2006). The gamma term was set to 1.4 to prevent over-fitting (Kim & Gu 2004). All models were computed as a binomial regression using the function 'gam' in the R package 'mgcv' (Wood 2015).

2.4 Results

Between 4 and 71 observations were made for each ground beetle species with on average 23 per species (Table 2.1). Realized interactions were observed in 54 % of the feeding tests for the 17 ground beetle species with ≥ 10 observations. Only four species had < 50 % of realized interactions with offered prey, including *Myas cyanescens* Dejean that did not interact with any of the 14 offered prey species. *Pterostichus caudicalis* Say was the species with the highest percentage (86 %) of realized interactions (12 interactions over 14 observations).

The best overall model had an accuracy of 83.4 %, a TSS of 0.65 and included three trait-matches (predator size/ prey size, predator mandibular strength/ prey cuticular toughness and predator eye size/ prey speed), two unmatched predator traits (length of the mandible and length of cutting section) and the phylogenetic term (Table E.1). All four aspects of the goodness of fit (accuracy, sensitivity, specificity and TSS) were significantly higher than both null models (SES>3.9, P<0.001). The 'best parsimonious' model was predator size/ prey size + predator mandibular strength/ prey cuticular toughness + phylogeny, with an accuracy of 81.4 % and a TSS of 0.61. This model also had significantly higher scores for the four aspects of the goodness of fit than for both null models (SES>3.7, P< 0.001) (Table 2.3). Adding the trait-match predator mandibular gape/ prey body width slightly increased the accuracy to 82.5 % and TSS to 0.63.

The best single trait-match model was predator strength/ prey cuticular toughness (accuracy = 71.5 % (SES=3.17, P<0.001); TSS = 0.37 (SES=2.92, P=0.002)), followed by predator mandibular gape/ prey body width (accuracy = 67.5 % (SES= 2.44, P= 0.007); TSS = 0.26 (SES= 1.94, P> 0.05)) and predator size/ prey size (accuracy = 66.4 % (SES= 2.24, P= 0.013); TSS = 0.23 (SES= 1.67, P> 0.05)) (Table 2.3). The model with predator strength/ prey cuticular toughness had a significantly higher accuracy, sensitivity and TSS than null models, but not specificity. The model predicted an increased probability of realized interactions between strong predators and hardened prey, but we found an abrupt threshold response around a cuticular toughness of 40 g mm^{-2}, following which no realized interactions were predicted (Figure D.2A).

Adding phylogenetic information increased the accuracy and the TSS of all models (Table E.1). It also had a strong positive impact on the specificity increasing it on average for all models by 24 %. For individual trait-matches and unmatched traits, the specificity increased by 29 % on average with the added phylogenetic term. When

taken alone, phylogenetic information (accuracy = 74 % (SES=3.61, P<0.001); TSS = 0.46 (SES=3.72, P<0.001)) had a better goodness of fit than any single trait-match model (Table 2.3).

Table 2.3 Goodness of fit of two null models, of the two best models out of 511 tested models (best overall and best parsimonious) and of all used terms tested individually (four trait-matches, four unmatched traits and a phylogenetic term) to infer ground beetle/ prey interactions observed in a feeding experiment. Null model 1 is a complete randomization of the observed interaction matrix while null model 2 is a randomization of prey species only. Values for the null models represent the lower and upper limit of a 95 % confidence interval for 10,000 iterations. "Best" is the model with the highest TSS without limit of terms while "Best parsimonious" is the model with the lowest number of terms and a similar TSS to the 'best' model. Significance of each goodness-of-fit aspect was determined by calculating standardized effect sizes (SES).

Model	Accuracy	Sensitivity	Specificity	TSS
Null models				
Null 1	40-63	43-73	24-60	-0.24-0.24
Null 2	51-62	53-76	28-59	-0.13-0.29
Best models				
Best†	83***	87***	78***	0.65***
Best parsimonious‡	81***	87***	74***	0.61***
Phylogeny	74***	78**	68**	0.46***
Trait-matches (predator/ prey)				
Mandibular strength/ cuticular toughness	71***	87***	49	0.37**
Mandibular gape/ body width	67**	89***	37	0.26
Body size/ body size	66**	92***	30	0.23
Eye size/ movement speed	60	84***	25	0.1
Unmatched predator traits				
Apical tooth	64	82**	38	0.2
Absorption	64	94***	22	0.16
Terebra	63	83***	36	0.18
Mandible	64	81**	39	0.2

*** SES > 3.09 (P<0.001) ** SES > 2.32 (P<0.01) * SES > 1.96 (P<0.05)

† Phylogeny + predator body size/ prey body size + mandibular strength/ cuticular toughness + eye size/ speed + length of the mandible (predator) + length of the terebra (predator)

‡ Phylogeny + predator body size/ prey body size + mandibular strength/ cuticular toughness

2.5 Discussion

We found that the matching-centrality formalism accurately predicted predatory interactions of ground beetles (Table 2.3). The combination of the phylogenetic term with trait-matches predator strength/ prey cuticular toughness and predator/ prey size ratio captured most of the variation of predator/ prey interactions observed in our experiments. This success demonstrated that combining these three terms could increase our ability to infer trophic interactions among arthropod and soil invertebrates better than considering predator/ prey size ratio alone. While predator/ prey size ratio is of common use, mandibular strength (or force bite) has rarely been considered when studying interactions of arthropods (but see Ibanez et al. 2013; Deraison et al. 2015 for herbivorous arthropod examples). It is, however, commonly used with vertebrates (e.g. Wroe, McHenry & Thomason 2005; Christiansen & Wroe 2007). The resistance of arthropod ecologists to use it is possibly due to the difficulty to measure the force of arthropod bites, but this could be circumvented by the use of allometries as used with extinct vertebrates (Wroe et al. 2005). Our study shows that these allometries are reliable, at least as a comparative tool, and can be used to successfully predict interactions between arthropods. Contrary to our expectation, predator strength/ prey cuticular toughness had an overall better goodness of fit than predator/ prey size (Table 2.3).

Phylogeny

No model accurately predicted unrealized interactions without the inclusion of phylogenetic information. While all the models with TSS higher than the null models predicted at least 80 % of realized interactions, none predicted more than 58 % of unrealized interactions (i.e. equal to the null models). This difference demonstrates

that realized interactions were easier to predict than unrealized interactions based on trait-matching only. The lack of replication for many interactions in the feeding experiment may have artificially increased the number of unrealized interactions, making them harder to predict. Furthermore, it is highly probable that unrealized interactions could be better predicted by including traits that reflect prey defense strategies, such as mucus secretion by slugs (Pakarinen 1994), fast jumping ability of springtails (Bauer & Kredler 1993) and deterrent chemical compounds (Eisner et al. 2005). However, chemical and other specialized defense strategies can be hard to quantify and thus to include in a trait-matching model. As these traits are generally shared with close relatives (Eisner et al. 2005), phylogenetic information can be useful to assess several aspects of predator/ prey interactions that cannot be accounted for easily with available trait data (Morales-Castilla et al. 2015).

Phylogeny in itself captures much of the variation explained by the traits (Table 2.3), which could suggest that using phylogeny alone would be more parsimonious. However, phylogeny is relevant only for species (or maybe genera) included in the present experiment, and does not bring any information on the mechanisms involved in prey selection. In contrast, the information gathered through trait matching is generalizable to other mandibulate arthropods and useful to understand food web structure (Morales-Castilla et al. 2015; Gravel et al. 2016a). Also, a phylogenetic analysis could miss relevant variation among close relatives. For example, it was shown that in tiger beetles (Carabidae: Cicindelinae), body size and length of the mandibles were unrelated to their phylogenetic position (Barraclough, Hogan & Vogler 1999). We see phylogeny as a useful tool helping to circumvent problems caused by the collection of important, but hard to measure, traits.

Trait-matching

The trait-match mandibular strength of predator/ cuticular toughness of the resource was the best predictor with ground beetles, but we expect it to be generalizable to other predators (Verwaijen, Van Damme & Herrel 2002), granivores (Abbott, Abbott & Grant 1975; Lundgren & Rosentrater 2007), herbivores (Ibanez et al. 2013) and potentially detritivores (David 2014). It provides a common currency, more generalizable than body size (Bartomeus et al. 2016) and thus, has potential to describe interactions of omnivorous species. Contrary to our original hypothesis, the trait-match mandibular gape of the predator/ body width of the prey did not bring significantly more information to the trait-matches mandibular strength of predator/ cuticular toughness, predator/ prey size ratio and the phylogenetic term. However, this trait-match is expected to be more important for predators that swallow their resources as a whole (Bremigan & Stein 1994), which were absent from our dataset. Similarly, the matching of the eye size of the predator and the movement speed of prey was hypothesized to be important to predict predation of ground beetles on springtails that often co-occur in the leaf litter layer (Bauer & Kredler 1993). However, this trait-match was also a poor predictor, possibly explained by the inclusion of only one truly big-eyed predator (*Notiophilus aeneus* (Herbst)). Despite that, it is of interest that *N. aeneus* was the sole species to successfully consume springtails in our experiment.

A novel tool to quantify predator-prey interactions

Our study brings a new tool to resolve cryptic food webs and could be generalized to a large array of organisms as all predatory interactions are determined by similar constraints; the ability to catch, handle, ingest and digest prey (Gravel et al. 2016a). Traits have been intuitively considered in the past to explain the occurrence, or the

absence, of interactions but our approach now formally integrates them into a predictive model. Thus, important traits identified in one system might also prove useful to understand the interactions in another one. For example, studies on rotifers revealed similar trait-matching limitations as we observed for ground beetles: catching ability was limited by prey speed, handling by physical defence, ingestion by prey length and digestion by chemical defence (Nandini, Pérez-Chávez & Sarma 2003; Deines, Matz & Jürgens 2009).

Nevertheless, other trait combinations will undoubtedly be required to predict interactions of predators with different foraging behaviour than ground beetles. Passive predators, as web spiders, use traps adapted to behavior of prey (Schmitz 2005). In the case of flying predators, traits related to flying maneuverability of both predator and prey (e.g. wing loading) could be matched to determine their probability of interactions (Chai & Srygley 1990, Combes et al. 2013). Similarly, swimming performance could be important to determine interactions in aquatic environments (Cooper, Smith & Bence 1985, McPeek, Schrot & Brown 1996). Beyond predator-prey interactions, for example in pollinator networks, one might consider the trait match of pollinator proboscis length/ depth of the corolla (Ibanez 2012) or to match the hairiness of different parts of the pollinator's body and the morphology of flowers (Stavert et al. 2016). The principal limitation in our capacity to extend such an approach, remains documenting more traits that restrict predator/ prey interactions, along with an extensive documentation of predatory interactions (and their absence).

Finally, our model incorporates scavenging, which allows access to high quality food acquired at a low energy cost for the predator and could be favorable to the maintenance of predator species without any cost for the species of the carrion (Wilson & Wolkovich 2011). Unfortunately, this information is frequently overlooked. Larochelle and Larivière (2003) report necrophagy observations for only 37 species of ground beetles in North America out of +2400 species. During our

feeding experiment, all 14 ground beetle species (only one already identified as necrophagous (Larochelle & Larivière 2003)) that were offered a dead prey ate it at least occasionally, revealing that scavenging could be an important aspect of their feeding habits (Table 2.1). Molecular techniques have permitted many advances in understanding food webs, but do not easily discriminate scavenging from predation and can include errors in food web analysis (King et al. 2008). Increasing the documentation of these interactions will be important to allow their prediction in natural food webs, although ideally separate models will be used to distinguish scavenging from more classic predatory interactions given that scavenging will not influence population dynamics of prey.

Perspectives

While our model identifies the potential feeding niche of ground beetles in the laboratory, the realized niche in a truly natural environment will vary from the potential niche due to food availability, higher-order interactions and varying abiotic conditions (Poisot, Stouffer & Gravel 2015). Akin to species distribution modeling where presence-absence has to be modeled distinctively to abundance because they respond to different drivers (Boulangeat, Gravel & Thuiller 2012), potential interactions and the strength of interactions should be considered separately. The interaction of two species in a natural environment will depend on the encounter probability of the species, the matching of their traits (Bartomeus et al. 2016) and the foraging ability of the predator. The biotic context could also influence the occurrence and the realization of interactions, for instance with another predator influencing the behavior of the prey or parasites reducing its ability to escape predation. While we focus exclusively on trait-matching and phylogeny in our model, future efforts should attempt to integrate other drivers of interaction strength. While there are promising methods to account for co-occurrence (Poisot et al. 2015; Gravel

et al. 2016b) and relative abundance (Poisot et al. 2015; Bartomeus et al. 2016), integrating foraging behavior may be more challenging. Integrating interaction strength is the next frontier and doing so, will require us to consider aspects such as the ability of a predator to optimize energy intake per handling time (MacArthur & Pianka 1966). It is still unclear which traits (if any) will correctly approximate energy intake and handling time, but traits such as predator/ prey body size ratio (Brose et al. 2008; Petchey et al. 2008) and biting force/ resource toughness (Verwaijen et al. 2002) could be important.

2.6 Conclusion

Species interactions influence species distributions at small and large spatial scale (Araújo & Rozenfeld 2014) which in turn have consequences for local ecological processes (Bartomeus et al. 2016). Thus, interaction networks need to be well understood to predict the consequences of species loss and species invasion caused by global change drivers. Our approach mixing traits and phylogenetic information offers a new opportunity to understand and infer accurately predatory interactions for species that are difficult to observe in the field. We demonstrate that traits such as the mouthpart strength of arthropod predators and corresponding prey cuticular toughness can help unravel their interactions. This trait-match is interesting as it is more generalizable than body size matching to infer antagonistic interactions including herbivory. The proposed approach could also be beneficial to infer other interactions such as mutualism, commensalism, etc. (Morales-Castilla et al. 2015). Adding data about species encounter probability and optimal foraging are suggested future steps to better predict food web interactions.

2.7 Acknowledgments

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CHAPITRE 3

MATCHING PALATABILITY TRAITS AND FEEDING TRAITS OF THREE TROPHIC LEVELS PARTIALLY EXPLAIN THE DISTRIBUTION OF ARTHROPODS IN FOREST LITTER.

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3.1 Abstract

The functional traits approach assumes that relating traits of organisms within a community to variation in abiotic and biotic characteristics of their environment will provide insight on the mechanisms of community assembly. This hypothesis is supported by a large amount of work in plant ecology, but has been less studied with animals. Traits at a given trophic level might act as filters for the selection of traits at another trophic level, and thus we can hypothesize that traits of the consumers and of their resource co-vary in space. We tested this hypothesis with litter-dwelling macroarthropods and their resources collected in three forested sites of southern Québec. Traits related to the palatability of leaf litter (toughness, thickness and water retention) and prey (body volume, body width and cuticular toughness) were measured as well as the feeding traits of decomposers and predators (including body volume, biting force, and size of the mouthparts). Our results showed that feeding traits of both decomposers and predators co-varied with the abiotic gradients (temperature and humidity) and leaf species found in the litter. Feeding traits of the consumers partially co-varied with the palatability traits of their resource, however co-variation between species identity at each trophic level was generally higher. Our trait-based co-variation results remain nonetheless interesting as they offer insight on the mechanisms involved in species assembly thus permit generalization across arthropods, i.e. traits of a trophic level can act as a biotic filter on the traits of other trophic levels. Including traits related directly to abiotic filters would probably further increase our ability to describe community assembly of arthropods.

3.2 Introduction

The study of functional traits relies on the hypothesis that the abiotic and biotic environmental characteristics act as filters selecting individuals based on their traits (Diamond 1975; Keddy 1992; Shipley 2010). Correspondingly, functional traits are any morphological, physiological, phenological or behavioural characteristic measurable at the individual level that can be related to the fitness of an organism (Violle et al. 2007; Pey et al. 2014b). Thus, relating traits represented in a community to the environmental conditions of that same community could provide insight on the mechanisms of community assembly. There is a large amount of work in plant ecology supporting this hypothesis (Lavorel et al. 2007; Reich 2014; Garnier, Navas & Grigulis 2016). In contrast, the use of a functional trait approach with animals has been slower to implement and much remains to be done (Luck et al. 2012; Pey et al. 2014b; Fountain-Jones, Baker & Jordan 2015; Moretti et al. 2016; see Chapiter 1). Filters selecting traits among animals are more complicated to disentangle, as traits at a given trophic level might act as filters for the selection of traits at another trophic level (Ibanez 2012; Lavorel et al. 2013). For instance, traits determining the foraging capacity of predator communities will act as filters of traits for the prey. Alternatively, the traits of the prey, such as chemical or physical defense, will also drive which predators could be present in a community. As a consequence, one could hypothesize that traits should co-vary among consumers and their resource.

The trait approach has been used with many animal taxa including fishes (Mouillot et al. 2013), zooplankton (Litchman, Ohman & Kiørboe 2013), nematodes (Cesarz et al. 2015), birds (Luck et al. 2012), beetles (Fountain-Jones, Baker & Jordan 2015), etc. Surprisingly, while feeding traits are largely studied in evolutionary and biomechanical studies (Manton & Harding 1964; Roberts 1970; Acorn & Ball 1991; Christiansen & Wroe 2007; Clissold 2007; Herrel et al. 2008; Smythe 2015), they are

rarely considered in studies using a functional trait approach. Studies considering feeding traits generally only consider the consumer perspective (Davies et al. 2007; Brind'Amour et al. 2011; Podgaiski et al. 2013), which means that the variation in trait values between communities is assumed to be related to resource variability instead to be formally tested. However, it could be more effective to look at both consumer and resource traits to better understand the importance of feeding interactions (Deraison et al. 2015; Le Provost et al. 2017). Examples of feeding traits include biting force (Wheater & Evans 1989; van der Meijden et al. 2012), and handling ability based on the mouthparts gape (Brodie & Formanowicz 1983; Cunha & Planas 1999). Nevertheless, they are hypothesized to play an important role in the structuring of animal communities (McGill et al. 2006; Hawes et al. 2009).

Understanding how feeding traits of various trophic levels are co-distributed in space is required to better understand the structure of the network of interactions, and eventually ecosystem processes such as pollination, trophic regulation or decomposition (Lavorel et al. 2013; Schleuning, Fruend & Garcia 2015; Gravel, Albouy & Thuiller 2016). Several studies have shown that the first condition for an interaction to occur is a match of traits between the consumer and the resource (see the review in Bartomeus et al. 2016). The second condition for this interaction to occur is that the species harboring these traits must encounter each other in space (Gravel, Albouy & Thuiller 2016). In other words, interactions are more likely to happen if these traits are positively co-distributed in space.

The distribution of the feeding traits in a community determining interguild interactions can be influenced by different processes. Firstly, the distribution of the feeding traits can be affected by abiotic conditions or dispersal ability irrespective of biotic interactions. For example, bees found in recently burned forests of Switzerland were shown to have shorter tongues than bees in unburned sites; however this observation is probably due to a correlation between tongue length and nesting sites

which are strongly affected by fire (Moretti et al. 2009). In such a situation, we could expect indirect trait associations between consumers and the resource, such that the trait of the consumer determining its response to the abiotic environment could be related to the traits of the resource determining their palatability. Secondly, feeding traits of consumers can co-vary in space with traits of their resources. If this particular interaction is of predator-prey type for instance, then a positive trait co-variation would imply a stronger trophic regulation. Similarly, if the interaction is rather plant-pollinator, then a positive trait co-variation would be responsible for higher plant productivity. An appropriate investigation of the functional structure of animal communities, involved in various types of ecological interactions, should therefore involve a quantification of the trait co-variance structure. The co-variance within guilds has been studied for some groups (Edwards & Stachowicz 2010; Astor, Lenoir & Berg 2015), what remains unknown is how traits co-vary across guilds, over space and environmental gradients.

Typical studies using the functional approach are based on the quantification of the average trait value (e.g. using community weighted means – CWM) and their variance (using a variety of approaches such as community weighted variance, functional dispersion or measures of evenness) (Swenson 2014). Community weighted means are commonly used to describe changes in functional composition along an environmental gradient (Wright et al. 2004; Chave et al. 2009) and represent the mean trait value for all measured organisms in a community. In a multi-trophic system, it could be hypothesized that a change in the CWM of a palatability trait of the resources will be reflected in the CWM of a matched feeding trait of the consumers. Thus if available prey are bigger, predators should also be bigger. Functional dispersion (FDis) represents the mean distance of measured organisms to the centroids of communities (Laliberté & Legendre 2010) and thus, it is a measure of the variation in trait values. It could be hypothesized that an increase in the FDis of

palatability traits of resources corresponds to an increase in niche availability for the consumers, which will be reflected in an increase of the FDis of their feeding traits.

In this study, we tested the hypothesis that palatability traits of available resources will influence the distribution of consumers based on their feeding traits evident through their co-variation in space. To do so, we studied the communities of macroarthropod detritivores and predators dwelling in forest litter and their respective resources. These communities were sampled at three different sites, each presenting a strong gradient in overstory tree composition. We analyzed the relationship between the feeding and palatability traits of decomposers and leaf litter, and of predators and prey. We first tested how the distribution of the feeding traits of the decomposers and the predators in a multi-dimensional space co-varied with the abiotic filters. Then we analyzed the co-variation of feeding and palatability traits in multi-variate space.

3.3 Material and Methods

Study sites

Sampling was carried out in three protected temperate deciduous forests of southern Québec (Parc national du Mont-St-Bruno, Gault Nature Reserve of Mont-St-Hilaire and Mont-Écho which is situated in the Montagnes Vertes ecological reserve). Sites at Mont-St-Bruno and Mont-St-Hilaire are separated by ~12.5 km while Mont-Écho is ~75 km south from them. Mont-St-Bruno (45°33'09"N 73°19'18"W) and Mont-St-Hilaire (45°32'59"N 73°09'39"W) are both epizonal inclusion from the Cretaceous age situated in the St. Lawrence Lowland (Feininger & Goodacre 1995) and are dominated by deciduous forests surrounded by agricultural and suburban development. The forest is mainly composed of *Acer saccharum*, *Quercus rubra* and

Fagus grandifolia. Other common trees in these sites include *Acer pensylvanicum*, *Fraxinus americana* and *Ostrya virginiana*. Average annual temperature from 2000-2012 is 7°C at both sites and average annual precipitation amount to 1071 mm (Environment Canada, 2016). Total precipitation over the sampling period (June, July, August) of 2011 and 2012 was respectively 331 mm and 211 mm. The Mont-Écho site (45°06'06"N 72°30'37"W) is part of the Appalachian Mountains and is dominated by mature forest of *A. saccharum* and *F. grandifolia* at low elevation, and *Abies balsamea* and *Betula* spp. at higher elevation. Some sections of the study site are also covered by high density of *Viburnum lantanoides* and ferns (mainly *Dennstaedtia punctilobula*). Average annual temperature from 2000-2012 is 6°C and average annual precipitation amounts to 1371 mm (Environment Canada, 2016). Total precipitation during the 2011 and 2012 sampling period was respectively 496 and 303 mm.

Plots

Ten sampling plots were installed at both Mont-St-Hilaire and Mont-St-Bruno, in three distinct stands dominated by *A. saccharum*, *Q. rubra* or *F. grandifolia* for a total of 30 plots per site. Plots were at least 40 m apart. A Hobo® data logger was installed at 1 m height in each plot to record temperature between June 23 and August 30 2012. Measurements were taken at hourly intervals. Soil humidity was measured at the center of the plot, identified by a pitfall trap, at each three sampling periods in the summer of 2012 with a Field Scout TDR 300 with 4 cm long rods.

Fifty plots were installed on Mont-Écho along two parallel transects (25 plots/ transect) covering an elevation gradient of 200 m and following the forest gradient between the *A. saccharum* and the *A. balsamea* stands. Plots were separated along

transects by 40 m. Temperature and humidity were recorded as in Mont-St-Bruno/ Mont-St-Hilaire at the end of each trapping period in June, July and August 2012.

Arthropods sampling

One multipher pitfall traps (Jobin & Coulombe 1988) was installed at each of the 110 plots and were continuously active from late June to late August 2011. Samples were collected each two weeks at Mont-St-Bruno/ Mont-St-Hilaire and each three weeks at Mont-Écho. Traps were active only during two consecutive weeks in June, July and August 2012. Pitfall traps were 12 cm in diameter and 16 cm depth. Ethyl alcohol (40 %) with 5 % of white vinegar was used as preservative.

Litter samples and the superficial millimetres of soil humus layer were collected adjacent to each pitfall trap (less than 1 m away) once in August 2011, and once during each trapping period in 2012. Sample volume was standardized as the volume that filled a closed plastic bag of 20.4 x 15.4 cm without any compaction. Microarthropods were extracted from litter samples using a Tullgren funnel method. Litter was placed in funnels (16 cm diameter) less than 24 h after their collection. Temperature was gradually increased over one week from ~20 to ~40°C by varying light intensity of 60 W light bulbs.

Vegetation characterization and functional traits

All leaves collected for the Tullgren extraction were visually identified to species when possible, and individually weighed to the nearest 0.01 g. Three functional traits related to leaf litter decomposability and palatability for detritivore arthropods were measured: leaf toughness, leaf thickness and water retention (Bernays 1998;

Makkonen et al. 2012; David 2014). All traits were measured on ten leaves (or the maximum number available in the samples) per species per stand at Mont-St-Bruno/ Mont-St-Hilaire, and at five evenly distributed elevations on Mont-Écho. Leaf litter was rehydrated by spraying water on them twice and keeping them in a closed box for 48 h before measuring traits. Leaf toughness (g mm^{-2}), defined as the pressure required to perforate the leaf, was measured with a Pesola® Medio-Line pressure set. Up to five measurements were taken per leaf and the average value was used in the analysis. Leaf thickness was measured with a microcaliper to the nearest µm. Water retention represented the mass of the hydrated leaf (measured after the rehydratation process) divided by the mass of the dry leaf.

Traits were measured on partially decomposed leaves and thus, most likely fallen the previous autumn. Partially-decomposed leaves were favoured to freshly senescent leaves because macro-detritivores as millipedes are known to prefer partly decomposed to fresh leaves (Wolters 2000; De Oliveira, Haettenschwiler & Handa 2010). Furthermore, leaf litter is highly modified during the first winter in temperate forests (Moore 1983; Uchida et al. 2005; Strukelj et al. 2012). Particularly, N concentration increases progressively during first year of decomposition because of microbial immobilization (Uchida et al. 2005; Strukelj et al. 2012). The freeze-thaw period also has a disruptive action on the litter facilitating the action of microorganisms and resulting in a decreasing in cellulose concentration and an increase of recalcitrant components as lignin (Wu et al. 2010). These processes could modify the physical resistance of leaves for arthropod communities living in the litter layer during the active plant growing season.

Arthropod identification and functional traits

All Diplopoda, Isopoda, Carabidae, Araneae and Opiliones caught in pitfall traps were identified to the species level. Larvae of Diptera, Coleoptera, Mecoptera and Lepidoptera were also identified as morphospecies. All macroarthropods (except winged Diptera and Hymenoptera) and snails found in Tullgren extractions were identified at species or morphospecies level (hereafter referred to as species). Species caught only once or twice in Tullgren extractions were not considered in the analysis unless their ecology clearly associated them to the soil food-web. For example, all Chilopoda and apterous Hymenoptera known to parasite soil arthropods were kept in the analysis irrespectively of their abundance, but rarely caught Lepidoptera caterpillars were removed as few are associated with dead plant material.

Feeding guild (detritivore, predator, herbivore, omnivore and parasitoid) of each species was determined based on the literature. Body volume, in mm^3, was evaluated based on shape, length, width and height of each species and used as a measure of body size representing both a palatability and a feeding trait. Cuticular toughness (representing a palatability trait) was measured using a Pesola® Medio-Line pressure set to which we added an entomological pin of size 2 (diameter = 0.45 mm). Toughness, in g mm^{-2}, was defined as the pressure required to break through the integument with the pin. A value of zero was given for very small and soft species while a value of 1 was given to small, but sclerotized species. For detritivores and predators, we also evaluated the biting force and the length/ width ratio of mouthparts (both representing feeding traits). A biting force index of mouthpart tip was measured based on the formula $h \times b/c$. For mandibulate arthropods, h was the width of the head behind the eyes (i.e. the attachment point of the muscles related to mandibles), b was the basal width of the mandible between the condyle and the insertion point of the adductor muscle, and c was the length from the condyle to tip (Wheater & Evans 1989; Clissold 2007). The biting force index of the molar plate was also evaluated for

Diplopoda and Isopoda by measuring *b* between the condyle and the insertion point of the abductor muscle, and *c* between the condyle and the mid point of the molar plate. For arachnids, *h* was the size (length x width) of the chelicerae, *b* was the basal width of the movable digit and *c* was its length (van der Meijden, Herrel & Summers 2010; van der Meijden et al. 2012).

Statistical analysis

Several pitfall trap samples were lost principally due to mammal disturbance or flooding, resulting in an unequal number of days per trap between plots. We removed from the analysis the plots that were active for less than 2/3 of the trapping periods. Overall, nine plots were removed (Table 3.1). The abundance of each species was summed in each plot and corrected to reflect a total of 93 days of trapping by applying the formula: 93 x abundance / trapping days, rounded to the upper whole number. Data for the decomposers and predators came almost exclusively from the pitfall traps, unless a species was found in the extraction, but not in the pitfall traps for a plot. These represent 74 mentions overall, mainly involving smaller species of spiders (39), millipedes (28) and ground beetles (6). In these cases, one specimen was added to the species abundance matrix to acknowledge the presence of the species. Prey included data from the pitfall traps and the Tullgren extractions; for this reason, we applied a Wisconsin double-standardization to the species abundance matrix of prey. The very large milipede species Narceus americanus was not considered as a prey as it is unlikely to be predated by any of our predators and would have artificially inflate the CWM and FDis of prey where the species is present.

We described the decomposer and predator communities with redundancy analysis (RDA) to determine if their feeding traits co-varied with environmental factors. The RDAs were performed on the standardized CWM and FDis of the decomposers and

predators per plots with temperature and humidity as environmental factors. Leaf litter composition was also included as an environmental factor by extracting the scores of axes explaining more than 10 % of the observed variation (i.e. the first three) of a principal component analysis (PCA). Finally, the CWM of each leaf palatability trait was included to describe decomposer communities. The same logic was used for predator communities, but the scores of a PCA on prey communities were also added. Three axes were also used to be symmetric with leaf litter, however, the variation explained was < 10 % for all axes. Also, the CWM of the palatability traits of the prey were used. All explanatory variables were standardized. The RDAs were also performed on species abundance matrices with Hellinger's transformation (Legendre & Gallagher 2001) to see if the same ecological factors influenced species and functional composition. The significant contribution of explanatory variables was assessed with permutation tests with 9999 iterations with the function anova in R.

The co-variation of feeding traits of the consumers and palatability traits of the resource was analysed in a multivariate space with Procruste co-inertia analysis. We first performed PCA on each standardized functional component (CWM and FDis) of the leaf litter, decomposers, prey and predators independently. The PCA were compared with a Procruste analysis with the function *protest* of the *vegan* library in R with 9999 iterations (Oksanen et al. 2013). The Procrustes were also used to compare the species composition of each trophic level to evaluate the relative descriptive strength of the communities based on their traits.

3.4 Results

Data description

We identified 16 species of leaves in litter samples. *A. saccharum* and *F. grandifolia* were the only tree species producing leaf litter common to all three sites. Other dominant leaf litter in Mont-St-Bruno/ Mont-St-Hilaire was from *Q. rubra* while *A. balsamea* and *Betula* spp. were dominant trees in Mont-Écho. The presence of *A. balsamea* and *Betula* spp. at Mont-Écho separate this site from others on the first axis of the PCA on leaf litter composition (Fig. 3.1A). The sites are more mixed up on axes 2 and 3 (Fig. 3.1B). Overall, 9663 adult decomposers (7505 Diplopoda and 2158 Isopoda) belonging to 20 species were caught (Table 3.1). The species richness was higher in the Mont-St-Bruno site (19 species) than in the other two sites (12 or less species). Carabidae were the dominant predator taxa in abundance with 14,013 specimens caught, but Araneae had the higher species richness with 122 species (Table 3.1). Species richness and abundance of Araneae was higher in Sutton than in other sites and the abundance was particularly low in Mont-St-Bruno. Inversely, Carabidae and Opiliones were more abundant in Mont-St-Bruno than in other sites, but the richness of Carabidae was higher in Mont-Écho. Finally, 4471 larvae (from which, 2471 come from Tullgren extraction of the litter) and other prey belonging to 232 species were caught. Most species (111) were caught five times or less overall. The PCA on prey species distribution reveals a separation of Mont-Écho from other sites on the first axis, and a separation of Mont-St-Bruno and Mont-St-Hilaire on the second axis (Fig 3.2A). Mont-Écho and Mont-St-Hilaire are similar on axis two, and all sites are similar on the third axis (Fig 3.2B).

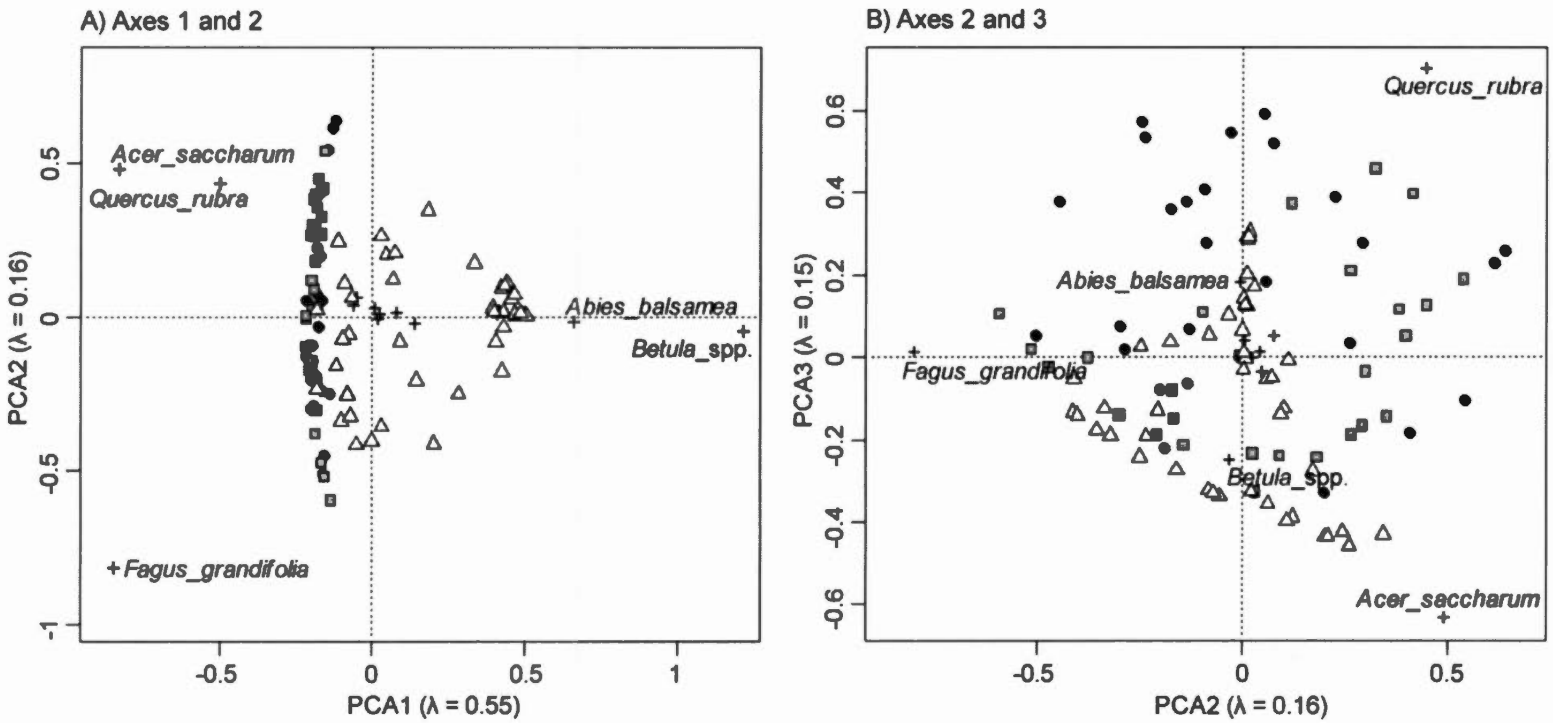

Figure 3.1 Principal component analysis (PCA) on the abundance of leaf species found in the forest litter in three sites in southern Québec: circle = Mont-St-Bruno; square = Mont-St-Hilaire; triangle = Mont-Écho.

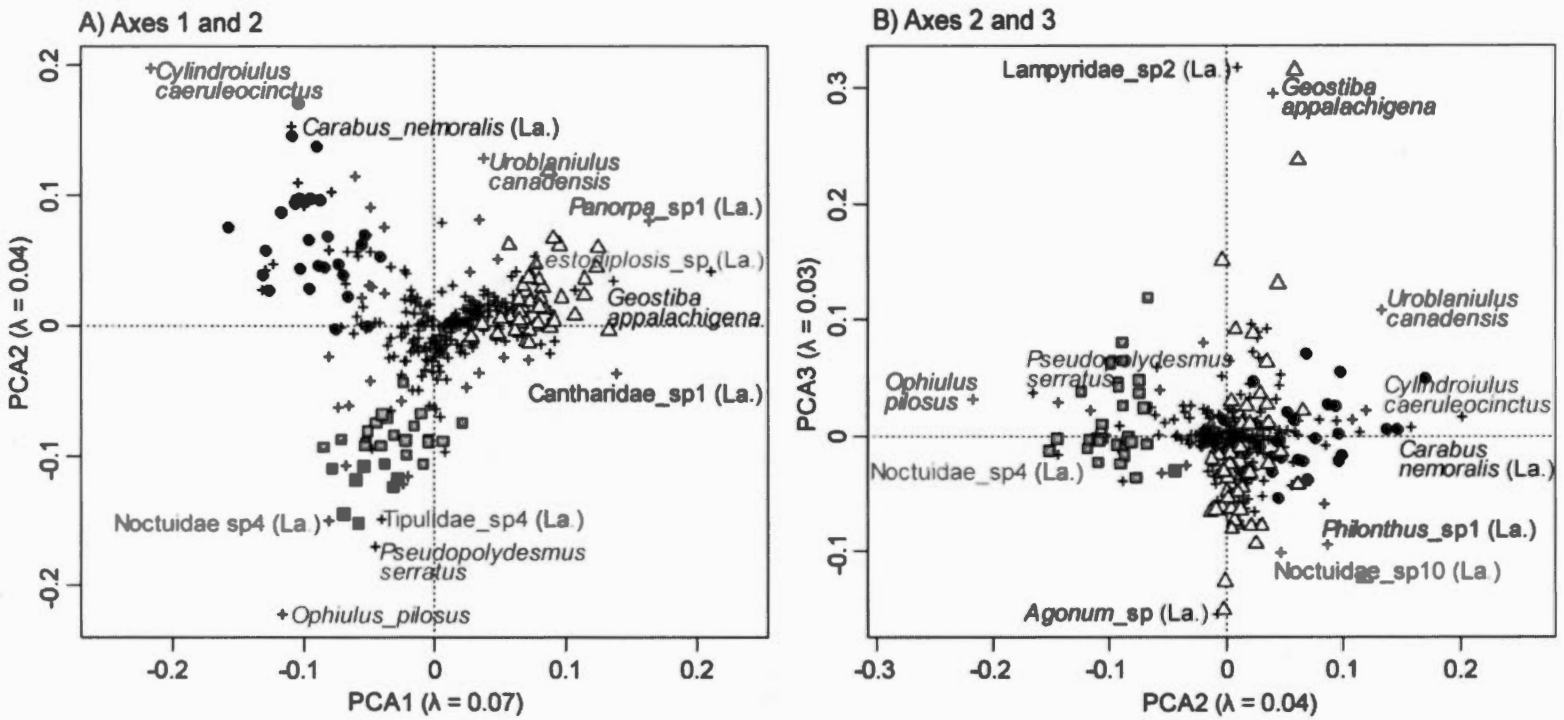

Figure 3.2 Principal component analysis (PCA) on the abundance of prey species found in the forest litter in three sites in southern Québec: circle = Mont-St-Bruno; square = Mont-St-Hilaire; triangle = Mont-Écho. Red = Diplopoda, Blue = Coleoptera, Green = Lepidoptera , Pink = Diptera, Dark green = Mecoptera. "(La.)" aside the name indicate a larval stage.

Table 3.1 Summary description of sampling sites.

		Mont St-Bruno	Mont St-Hilaire	Mont Écho	All
Plots	Number	27	28	46	101
Leaf litter	Richness	8	6	9	13
Diplopoda	Abundance	3245	3425	835	7505
	Richness	15	9	9	16
Isopoda	Abundance	1950	207	1	2158
	Richness	4	3	1	4
Carabidae	Abundance	5093	4050	4870	14013
	Richness	21	26	32	45
Araneae	Abundance	1261	2322	3380	6963
	Richness	60	59	77	122
Opiliones	Abundance	686	313	294	1293
	Richness	10	10	9	16
Other prey	Abundance	1022	1202	2247	4471
	Richness	123	144	160	232

Sites are generally well separated based on their mean recorded temperature. At Mont-Écho, mean temperature per plot varied between 16.4 and 19.1°C and are constantly colder than other sites. Mean temperature also tend to be slightly lower at Mont-St-Hilaire (19.9 - 20.8°C) than at Mont-St-Bruno (20.7 - 21.4°C). The variation of the humidity is larger within than across sites, with highest humidity recorded in Mont-Écho. Within site variation in humidity ranged between 3 - 14 % at Mont-St-Bruno, 4 - 17.2 % at Mont-St-Hilaire, and 4.5 - 37.7 % at Mont-Écho.

Co-variation between environmental factors and feeding traits

Arthropod decomposer communities, irrespective of whether described by species composition, CWM or FDis, were significantly explained by temperature, structure of leaf litter communities and the CWM of leaf litter toughness (Fig. 3.3A and 3.4, Table 3.2). The first PCA axis of the leaf litter community was correlated with thicker leaf litter, while axes 2 and 3 were correlated with tougher leaf litter. Decomposer

communities (described by species composition or Fdis) were significantly correlated to the CWM of leaf litter thickness (Table 3.2). Arthropod decomposer traits (body volume, biting force, mandible size and mandibular gape) co-varied with each other and with leaf litter toughness. The biting force of the molar plate co-varied with water retention of leaf litter and soil humidity (Fig. 3.4). Species communities of arthropod decomposers were well separated on the first two axes showing distinct communities at the three sites. This separation was less clear when the CWM or the FDis was analysed, but plots in Mont-St-Bruno still tended to be distinct from the other two sites.

Table 3.2 Summary statistics (F-value and statistical significance) of Redundancy Analysis (RDA) performed on decomposer communities. Species composition, community weighted mean (CWM) and functional dispersion (FDis) of five feeding traits (body volume, mandibular gape, biting force at the tip of the mandibles, biting force of the mortar region of the mandibles, and the length/width ratio of the mandibles) are compared.

Explanatory variables	Species	CWM	FDis
Humidity	1.8	0.4	0.4
Temperature	15.4***	4.4*	5.3*
Leaf litter community (PC1)	5.6***	6.3**	11.6**
Leaf litter community (PC2)	1.8	3.8*	2
Leaf litter community (PC3)	4.6***	13.3***	13.4***
Leaf litter thickness CWM	3*	1.4	5.7*
Leaf litter toughness CWM	2.8*	4.9*	7.7**
Leaf litter retention CWM	1.4	0.3	1
Total variation explained	0.54	0.33	0.5

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

The explanatory variables significantly related to the arthropod predator communities varied depending on whether one considered species composition, the CWM or functional dispersion of their feeding traits (Table 3.3). Species structure of predator communities were described by soil humidity and temperature, by all three PCA axes of the leaf litter community and by one PCA axis of the prey community (Fig 3.3B). In contrast, both CWM and FDis of predator traits were better described by the prey

community structure, with a small contribution of leaf litter community structure (for FDis) and temperature (for CWM). Predator traits body volume and biting force co-varied with the presence of prey with tougher cuticle for the CWM, and with prey toughness and body width for the FDis (Fig. 3.5). The predator trait mandibular length/ width ratio co-varied negatively with body volume and body width of prey when its CWM was considered, and was orthogonal to all prey traits when its FDis was considered. As observed in the decomposer communities, predator communities were distinct among the three sites when species composition was considered, but sites tended to be less distinct when functional composition (CWM or FDis) was considered (Fig. 3.5).

Table 3.3 Summary statistics (F-value and statistical significance) of Redundancy Analysis (RDA) performed on predator communities. Species composition, community weighted mean (CWM) and functional dispersion (FDis) of five feeding traits (body volume, biting force and the length/width ratio of the mandibles) are compared.

Explanatory variables	Species	CWM	FDis
Humidity	2.5^{*}	0.9	2.1
Temperature	4.7^{***}	11.8^{***}	2.3
Leaf litter community (PC1)	4.3^{**}	2.7	2.7
Leaf litter community (PC2)	2.1^{*}	2.5	3.1^{*}
Leaf litter community (PC3)	2.6^{*}	6.8^{**}	1.9
Prey community (PC1)	1.9	1	4^{*}
Prey community (PC2)	11.1^{***}	34.8^{***}	19.1^{***}
Prey community (PC3)	1	0.1	1
Prey volume (CWM)	1	2.2	2.3
Prey width (CWM)	1.2	2	2.3
Prey toughness (CWM)	0.8	0.7	0.4
Total variation explained	0.55	0.54	0.42

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

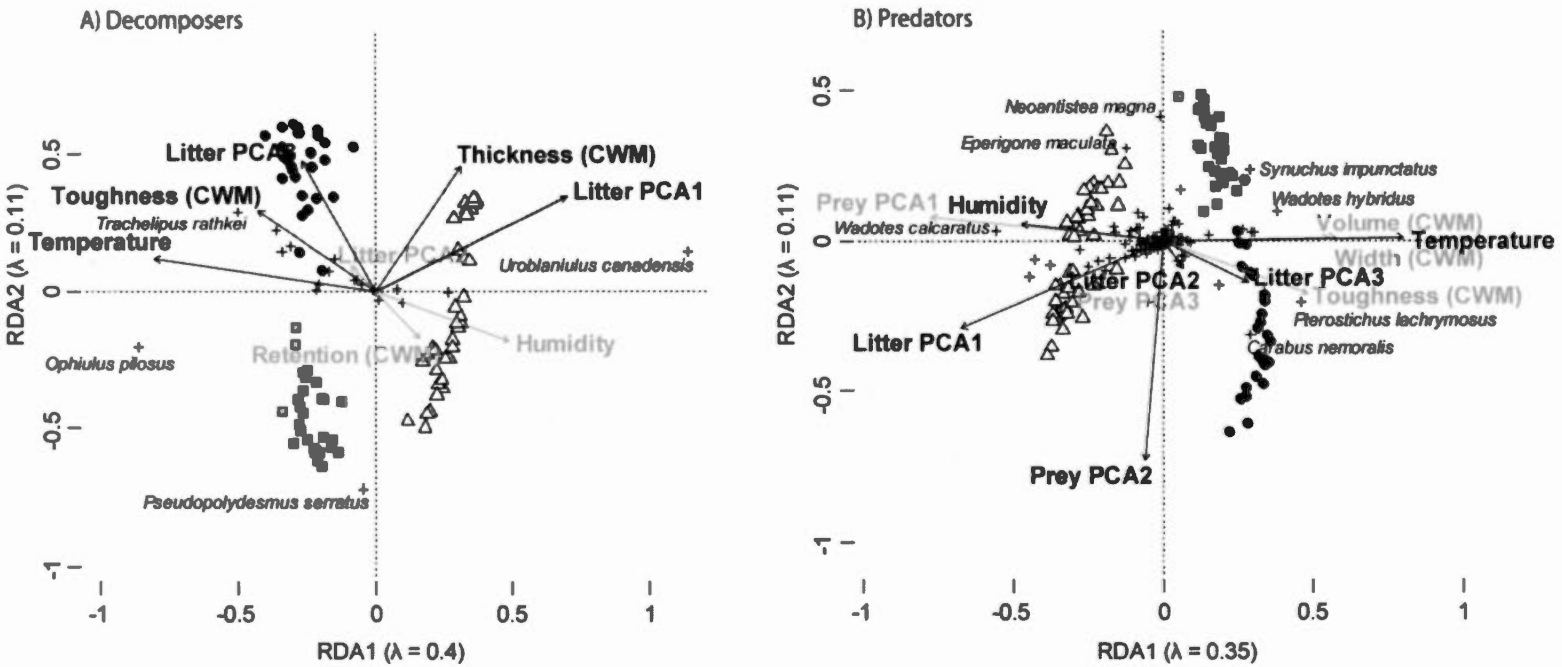

Figure 3.3 Redundancy analysis on the distribution of decomposer and predatory arthropods species of forest litter sampled in three sites in southern Québec: circle = Mont-St-Bruno; square = Mont-St-Hilaire; triangle = Mont-Écho. Blue arrows = significant variables based on permanova.

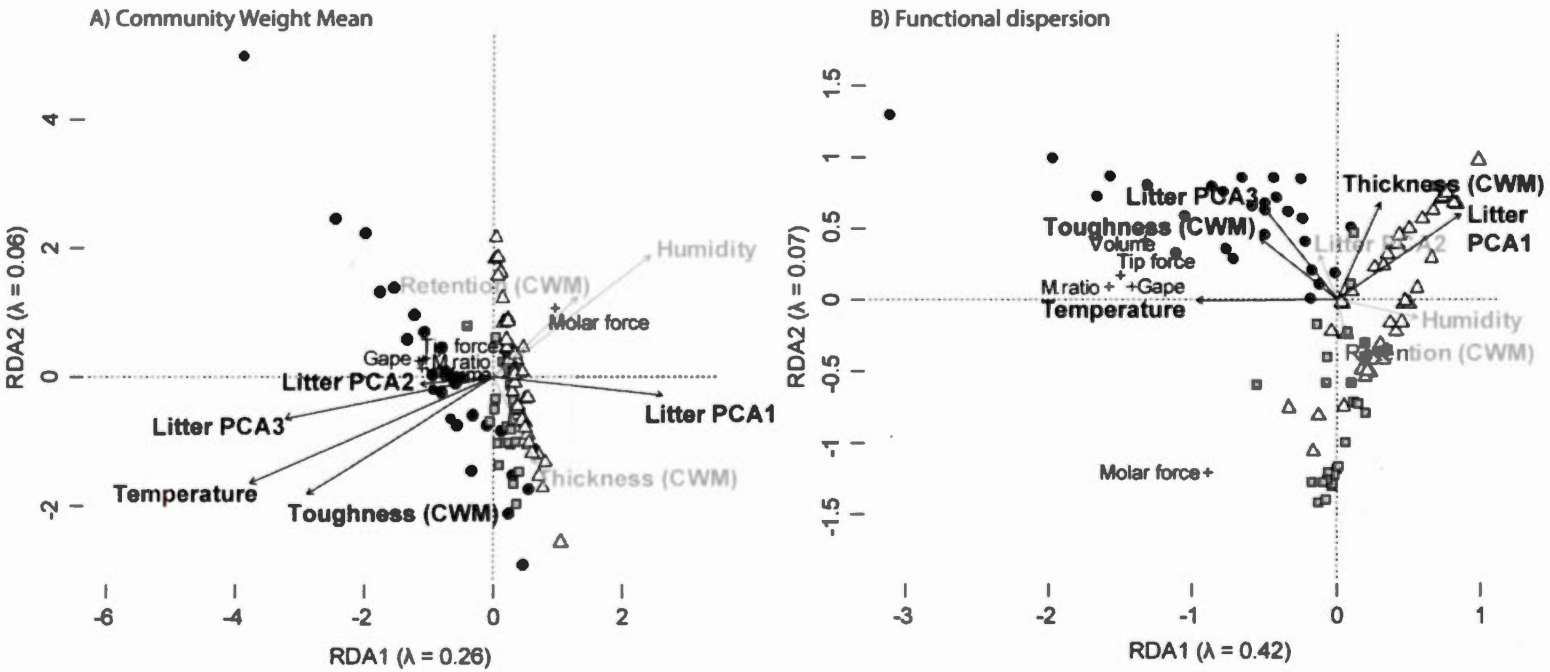

Figure 3.4 Representation of RDA on the distribution of five feeding traits of decomposer arthropods of forest leaf litter sampled in three sites in southern Québec based on their Community Weight Mean (CWM) and functional dispersion (FDis): circle = Mont-St-Bruno; square = Mont-St-Hilaire; triangle = Mont-Écho. Blue arrows = significant variables based on permanova.

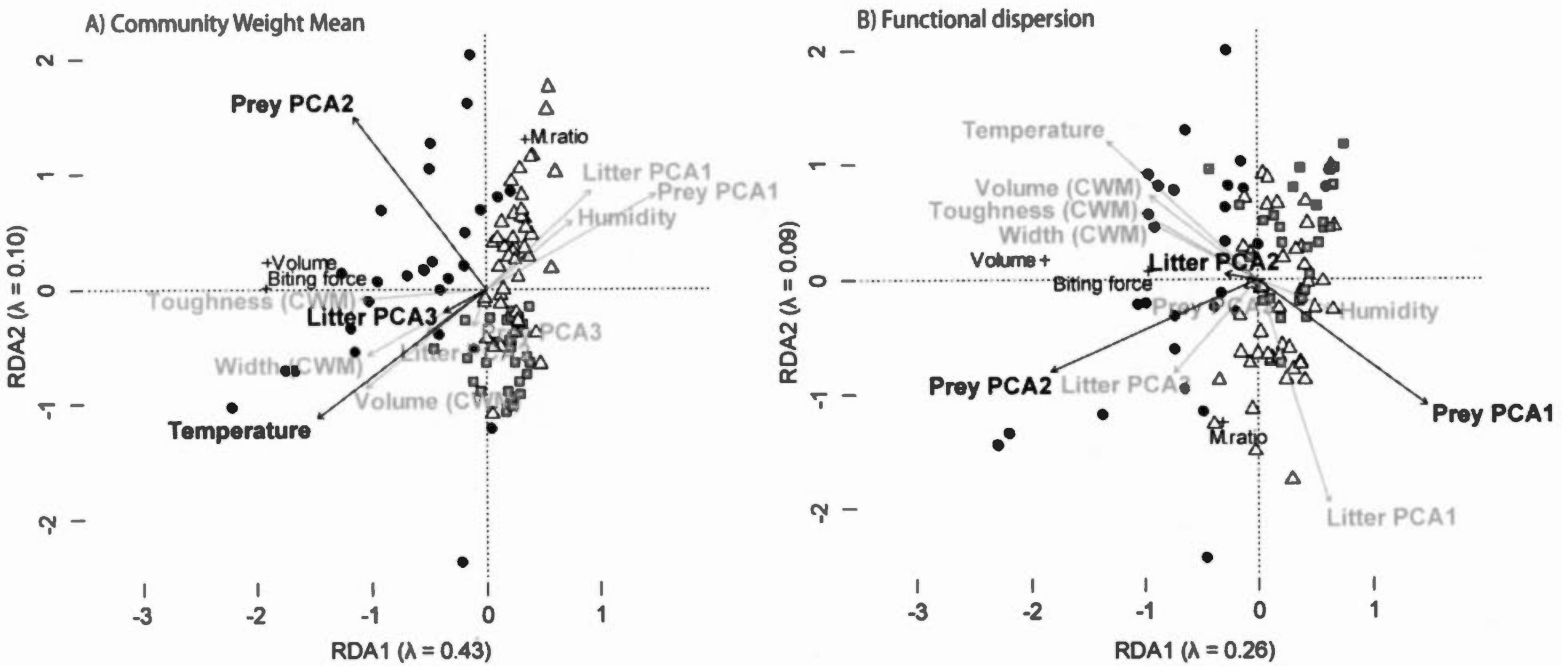

Figure 3.5 Representation of RDA on the distribution of three feeding traits of predatory arthropod communities of forest leaf litter sampled in three sites in southern Québec based on their community weight mean (CWM) and functional dispersion (FDis): circle = Mont-St-Bruno; square = Mont-St-Hilaire; triangle = Mont-Écho. Blue arrows = significant variables based on permanova.

Co-variation in multivariate space

Arthropod decomposer body volume co-varied consistently with leaf litter toughness for both CWM and FDis when sites were considered all together or separately except for the FDis in Mont-Écho (Fig 3.6 and 3.7). No other consistent co-variance was observed between feeding and palatability traits. All Procrustes analyses between arthropod decomposer communities and leaf litter communities were significant except for the CWM at Mont-St-Hilaire (Table 3.4). The correlation between the PCA of the CWM and the FDis of palatability traits of leaf litter communities and feeding traits of arthropod decomposer communities was similar (~0.3) when all three sites were considered together. However, the correlation between the PCA of these two communities was higher (0.6) when species composition was used to describe community structure. The correlation between the FDis was generally higher than the CWM when the sites were analysed separately, and it was also higher than for correlations between communities described with species composition in Mont-St-Bruno.

Table 3.4 Correlation between the PCA of the functional structure (community weighted mean (CWM) and functional dispersion (FDis)) and species structure of arthropod decomposers and leaf litter communities, and arthropod predators and prey communities based on Procruste analyses.

	Species	**CWM**	**FDis**
Decomposers / litter			
All sites	0.6^{***}	0.29^{**}	0.3^{***}
Mont-St-Bruno	0.42^{***}	0.39^{*}	0.52^{**}
Mont-St-Hilaire	0.49^{**}	0.26	0.34^{*}
Mont-Écho	0.57^{***}	0.32^{*}	0.33^{*}
Predators / prey			
All sites	0.72^{***}	0.4^{***}	0.26^{**}
Mont-St-Bruno	0.81^{***}	0.25	0.35
Mont-St-Hilaire	0.87^{***}	0.37^{*}	0.24
Mont-Écho	0.82^{***}	0.17	0.23

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

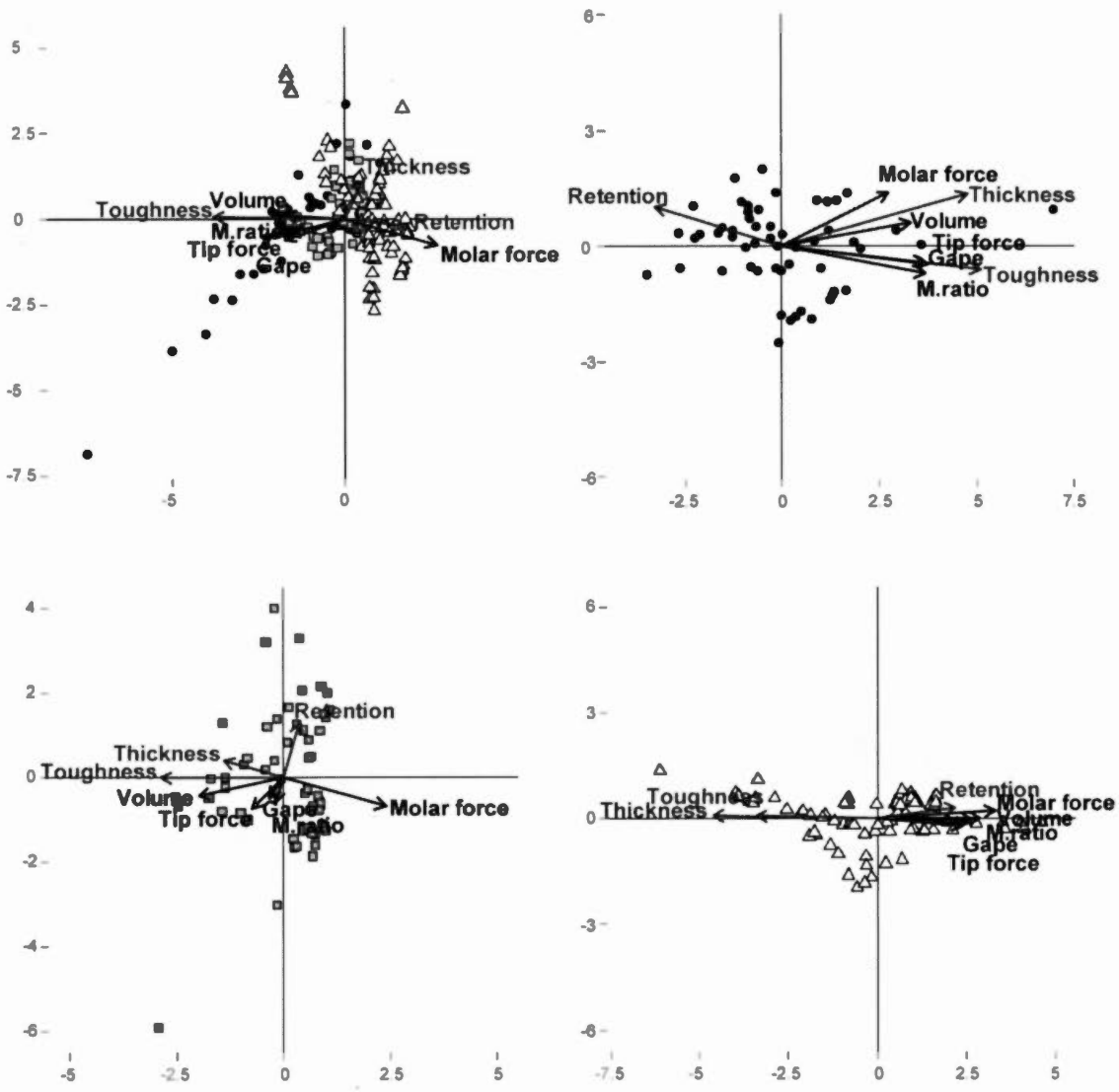

Figure 3.6 Procruste analyses on the community weighted mean (CWM) of three palatability traits of leaf litter (red arrow) and five feeding traits (blue) of arthropod decomposers in three sites of southern Quebec, or for each site separately: circle = Mont-St-Bruno; square = Mont-St-Hilaire; triangle = Mont-Écho.

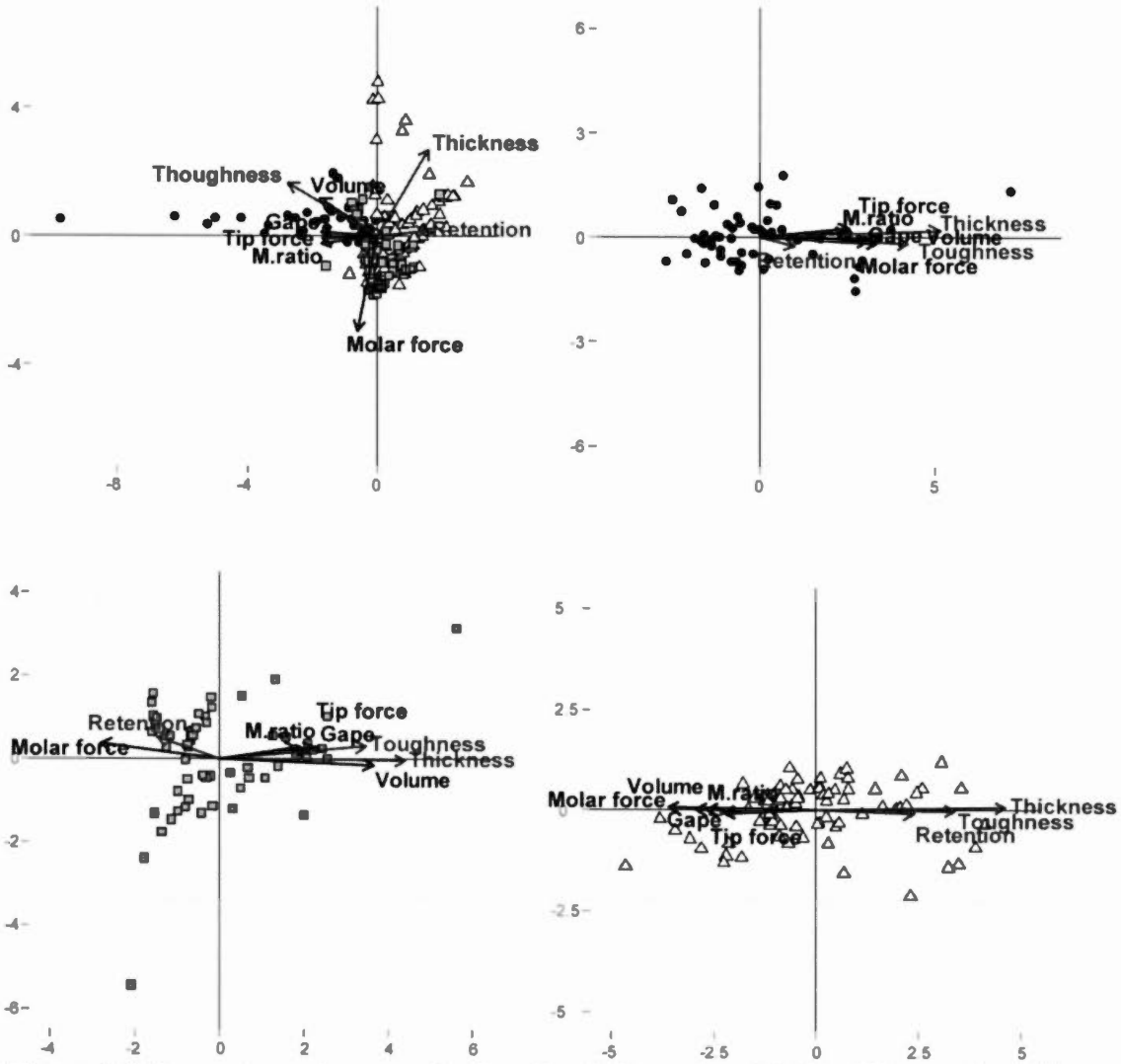

Figure 3.7 Procruste analyses on the functional dispersion (FDis) of three palatability traits of leaf litter (red arrow) and five feeding traits (blue) of arthropod decomposers in three sites of southern Quebec, or for each site separately: circle = Mont-St-Bruno; square = Mont-St-Hilaire; triangle = Mont-Écho.

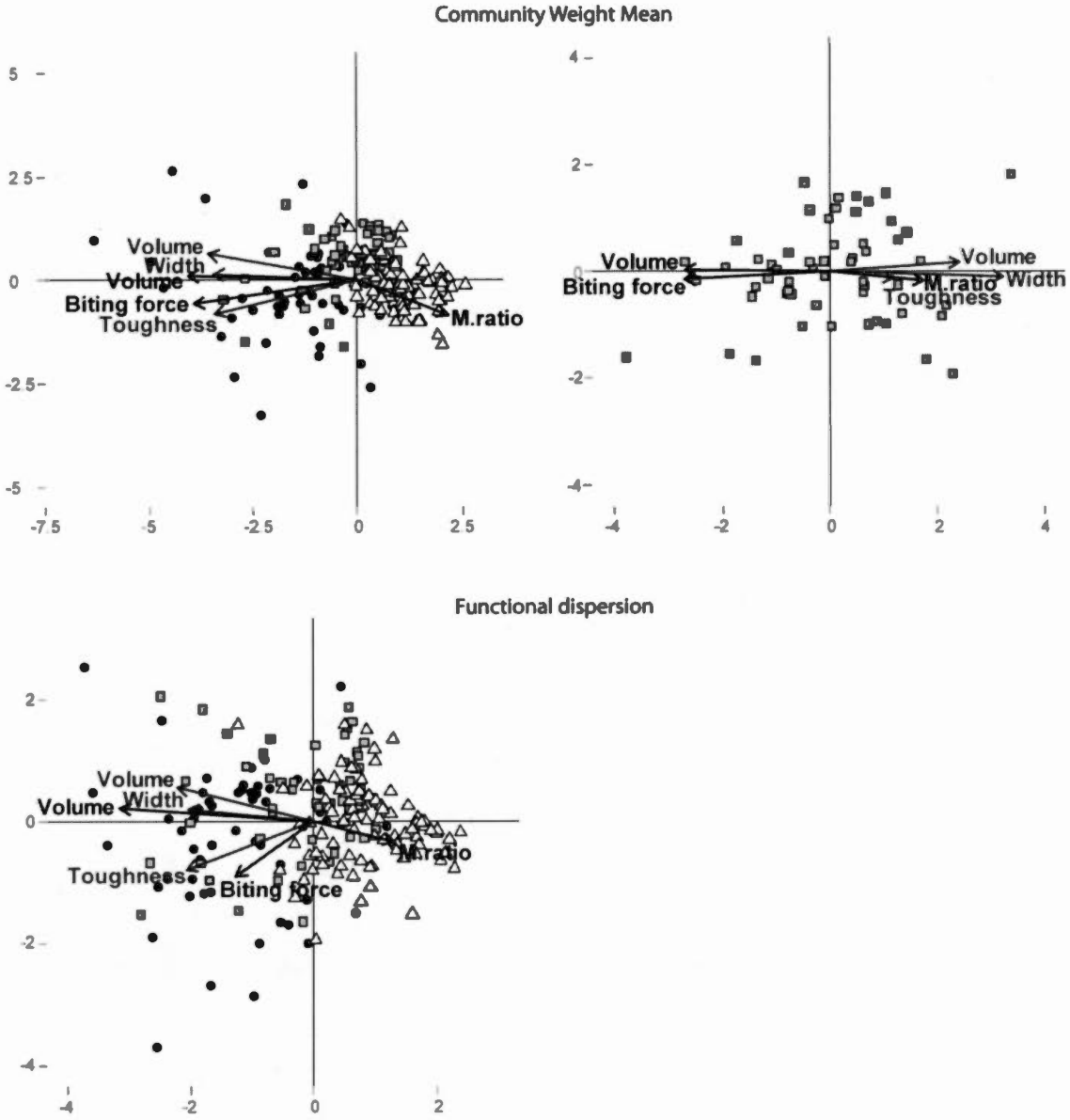

Figure 3.8 Procruste analyses on the community weighted mean (CWM) and functional dispersion (FDis) of three palatability traits of prey (red arrow) and three feeding traits (blue) of predators in three sites of southern Quebec, or for each site separately: circle = Mont-St-Bruno; square = Mont-St-Hilaire; triangle = Mont-Écho. Only significant analyses are shown.

Predator biting force and prey cuticular toughness, and body volume of both predator and prey communities co-varied positively for both CWM and FDis when all sites were analysed together; however, they co-varied negatively when the CWM of Mont-St-Hilaire was analysed alone (Fig. 3.8). The correlation between the PCA of the CWM and FDis of prey traits and predator traits was significant only when all sites were analysed together and for the CWM at Mont-St-Hilaire (Table 3.4). As for correlations between leaf litter and arthropod decomposer communities, the correlation describing species composition of arthropod predator and prey communities was always high (>0.7).

3.5 Discussion

Our results provide new insight on how feeding traits of arthropods co-vary with environmental factors and the palatability traits of their resources. We show that in the litter layer of deciduous temperate forests in southern Québec, the variation in species composition, functional composition (express as the CWM) and functional variance (express as the FDis) of arthropod decomposer communities is best explained by the same factors, but in different proportions. Thus, variation in temperature at the micro-site scale best described species composition of communities, but the functional characteristics of arthropod decomposer communities were better explained by leaf litter species and functional structure. Similar results were observed for arthropod predator species and functional composition, with prey species composition influencing the functional structure strongly of predators. However, there was no apparent link between the functional structure of predators and prey. A co-variance in the distribution of the palatability traits of the resources and the feeding traits of the consumers was observed with Procrustes analyses. However, correlations between species composition of communities were generally

higher than between functional composition, except for the decomposer community and the leaf litter in Mont-St-Bruno. Finally, results comparing functional composition (CWM) and functional variance (FDis) of communities were generally similar.

Determining factors influencing the distribution of functional traits in a community is a prerequisite to make the approach effective and to permit predictions (McGill et al. 2006). Our results show that our communities are better described based on species identity than on the selected traits. However, the results based on the traits are still more interesting as they permit generalization and prediction (McGill et al. 2006; see Chapiter 1). In our sites, we found that the millipede species Narceus americanus and Oriulus venustus tend to be associated with the presence of Q. rubra, but this result is only interesting for sites where these species co-occur. On the other hand, the observation that the biting force of the decomposers co-varied with the toughness of the leaf litter is probably still relevant in a forest where none of these species are present. Such co-variance can have an impact on the food web structure (Gravel, Albouy & Thuiller 2016). Thus, our results help to understand how soil food webs are structured and with some refinements, the study of feeding traits could provide an interesting tool to understand food webs dynamic (Morales-Castilla et al. 2015; Gravel, Albouy & Thuiller 2016).

Environmental factors

The abiotic factors we measured only had a small influence on the functional composition of decomposers and predators. The only consistent co-variation was found between soil humidity and the CWM of the length/ width ratio of the mouthpart for both trophic levels. It is not surprising as the traits were selected to reflect the feeding interactions of arthropods, not their abiotic interactions. Otherwise,

some co-variations were observed between the temperature and some traits, but it probably reflected the variation in term of species composition in the three sites instead of a real co-variance. In our study, temperature represented inter-site variation, while humidity represented intra-site variation. This interpretation could explain why temperature was a better descriptor of the macroarthropod communities over humidity, contrary to expectation, but the low number of sites cannot permit to confirm it.

Trait matching

In the decomposer-litter trait match, the only consistently observed co-variation (i.e. across analyses and in all sites, but Mont-Écho) was between the leaf litter toughness and the biting force of decomposers. The biomechanical co-variation between the biting force of the decomposers and the toughness of used resources was poorly studied, but studies on grasshoppers reveal that leaf toughness can act as a physical barrier restraining interactions (Ibanez et al. 2013). Our results suggest that this limitation is reflected in the distribution of the decomposers. Similar results were observed between the leaf toughness of living plants and biting force of grasshoppers (Le Provost et al. 2017). Interestingly, biting force of the predator and the cuticular toughness of the prey also co-varied in the uni- and multidimensional spaces. Body volume of predators and prey also co-varied across sites. While the body size ratio is a well known limitation of predator/prey interactions (Stouffer, Rezende & Amaral 2011; Gravel et al. 2013), the biting force/ toughness match is not well studied, but could be a better predictor than body size (see Chapiter 2).

Predators vs. decomposers

We observed that correlations between trophic levels were higher at the fine scale (traits are more correlated when sites are analysed separately) for decomposers (Fig. 3.6 and 3.7) and at a coarser scale (traits are more correlated when sites are analysed together) for predators (Fig. 3.8). This difference can be explained by the fact that predators are in general more mobile than decomposers (David & Handa 2010) and thus are expected to be less dependent on the conditions at the plot scale. Also, the arthropod prey community is far more complex than the leaf litter and harder to sample. It would have been highly complex to sample, identify and measure traits of all potential prey, thus we limited data collection to two trapping techniques and identification to un-winged macro-arthropods and snails. We are aware that this methodological choice may have limited our ability to describe the distribution of the feeding traits of the predators.

Species vs. traits

The spatial co-variation between consumers and resources was generally stronger for species composition than for functional structure. This can be explained by the fact that we only considered feeding interactions, while abiotic filters also play an important role in structuring arthropods of the forest litter (Frouz et al. 2004). RDA analyses also reveal that soil humidity and temperature influence the structure of species communities. However, we are still lacking morphological traits that can be related to abiotic factors with arthropods (see Chapiter 1). Some researchers circumvent the problem by integrating ecological traits describing species niche (e.g. Moretti et al. 2010), but these are not characteristics directly measured on the organisms (Violle et al. 2007), and are subject to circular reasoning. In some circumstances, phylogeny can be used to compensate missing information about hard

to measure traits (Webb et al. 2002; Cadotte, Albert & Walker 2013). However, phylogeny does not provide information on the direct mechanism contrary to functional traits.

3.6 Conclusion

Our results show that the traits of interacting trophic levels (litter/ decomposers and predator/ prey) co-vary in space. Interestingly, similar results were observed in a different ecosystem between plants/ herbivores with equivalent traits (leaves toughness/ biting force) (Le Provost et al. 2017). Such information could have an impact on food-web structure and temporal dynamic (Gravel, Albouy & Thuiller 2016). In our data, the strength of the co-variation between the resource and the consumer traits varied based on the trophic level and the study site. These differences could be explained by community complexity (species richness, functional diversity) or co-variation between dispersal or abiotic response traits and palatability/ feeding traits. This point out the need to develop reliable traits to assess the dispersal ability and abiotic interactions of arthropods to better understand species assembly processes and food-web structure. A next step would be to determine if the divergence in the strength of the co-variation between resource and consumer traits are reflected in food-web properties as connectance or nestedness.

3.7 Acknowledgments

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CONCLUSION GÉNÉRALE

L'objectif principal de cette thèse était d'identifier des traits fonctionnels généralisables à un grand nombre de taxa et permettant d'augmenter notre compréhension des mécanismes impliqués dans la formation des réseaux trophiques et l'assemblage des espèces. La revue de littérature du chapitre 1 a permis d'identifier quelques lacunes dans l'utilisation de l'approche par traits fonctionnels avec les arthropodes terrestres. Nous y présentons un cadre théorique dédié principalement aux entomologistes néophytes avec l'approche fonctionnelle, mais aussi pertinent pour une plus large part d'écologistes. Ce cadre devrait contribuer à améliorer la généralisation de l'approche par traits fonctionnels avec les arthropodes. Nous y présentons également l'intérêt des traits biomécaniques qui représentent des contraintes physiques influençant l'écologie des animaux et généralisables à un grand nombre de taxa, mais rarement utilisé jusqu'à maintenant. En ce basant sur l'idée des traits biomécaniques, un nouveau modèle incluant à la fois le principe du couplage de traits entre prédateurs et proies et les relations phylogénétiques des espèces est présenté dans le chapitre 2. Ce modèle est intéressant puisqu'il permet de prédire autant les interactions réalisées que celles non réalisées; un aspect souvent négligé dans la construction des réseaux trophiques, mais qui permet d'identifier les contraintes d'interactions. Cette étude a également permis de faire ressortir l'importance du couplage de trait force des mandibules du prédateur / dureté de la cuticule de la proie; un couplage également utile pour prédire les relations plantes/ herbivores. Les résultats du chapitre 3 démontrent que la structure fonctionnelle d'un niveau trophique influence partiellement la structure fonctionnelle au niveau suivant. Les traits utilisés pour prédire les interactions des carabes sont donc également utiles pour étudier l'assemblage des espèces. De plus, nous observons que la covariation entre les décomposeurs et la litière s'explique mieux à petite échelle (entre les parcelles), alors qu'elle s'explique mieux à grande échelle (entre les sites) pour les

prédateurs, qui sont plus mobile, et leurs proies. Ces résultats seront utiles pour mieux comprendre la dynamique des réseaux trophiques. Finalement, un aspect secondaire, mais non négligeable, de ma thèse est d'offrir une meilleure connaissance de la faune du Québec de certains groupes taxonomiques comme les diplopodes et les opilions (Appendices A et B).

Approche taxonomique vs. fonctionnel

L'approche par traits fonctionnels demeure peu développée avec les arthropodes et une des raisons semble être la réticence de plusieurs entomologistes à l'utiliser. En particulier, certains semblent voir l'approche comme réductionniste par rapport à l'approche taxonomique traditionnelle. L'approche par traits fonctionnels est présentée comme une approche "transcendant la notion d'espèce" (McGill et al. 2006), mais n'exclut pas pour autant l'aspect taxonomique. Les deux approches ont comme visées des aspects différents de l'écologie. L'approche taxonomique sert à décrire les changements observés dans les communautés suite, par exemple, à une perturbation. L'approche fonctionnelle sert plutôt à identifier les mécanismes responsables de ces changements et leur impact sur les processus écosystémiques. D'un point de vue de conservation, l'approche taxonomique va généralement être préférable, bien que les traits fonctionnels peuvent être utilisés pour identifier les espèces les plus à risques de voir leur population diminuer (Kotiaho et al. 2005, Comont et al. 2014). De plus, la pérennité des données de traits fonctionnels est fortement limitée si les traits ne sont pas couplés à l'identité des espèces. Mesurer les traits est une tâche qui peu être lourde et il est souvent impossible de prendre des mesures sur un très grand nombre de spécimens. Les études sur les végétaux démontrent que la variabilité intraspécifique dans les valeurs de traits est une composante importante de la structure fonctionnelle des communautés et que négliger cet aspect peu réduire l'exactitude des résultats (Jung et al. 2010, Albert et al. 2012,

Violle et al. 2012). De plus, connaître la variation intraspécifique pourrait être important pour pouvoir prédire adéquatement la distribution des espèces (Laughlin et al. 2012). Or, pour pouvoir déterminer la variabilité intraspécifique, un grand nombre de spécimens provenant de plusieurs populations est nécessaire, ce qui requière un effort collectif, des bases de données en libre accès et des méthodes de mesures standards des traits. Les deux premières exigences ne peuvent pas être remplies sans une identification à l'espèce.

Variation intraspécifique

La variation intraspécifique peut s'exprimer de deux façons: premièrement, il y a une variation reliée à la génétique et aux phénotypes qui devrait suivre une courbe standard avec la majorité des individus présentant une valeur moyenne et quelques rares individus présentant les valeurs extrêmes. Deuxièmement, il y a une variation reliée au stade de développement (Violle et al. 2012) pour laquelle la représentativité des valeurs de traits sera plus élevée au premier stade de développement et va diminuer progressivement selon le taux de mortalité à chaque stade. Cet aspect à un impact direct sur la structure fonctionnelle dans le temps et sur les interactions interspécifiques, mais peu être difficile à investiguer. Ainsi, nous pouvons émettre l'hypothèse que les traits reliés aux stratégies de développement ont un impact sur la structure temporelle des réseaux trophiques; e.g. l'impact temporel de la variabilité intraspécifique sera plus faible chez les espèces où les différents stades de développement se côtoient que pour les espèces univoltines. Due à des limitations techniques, cet aspect n'a pas été considéré dans les analyses du chapitre 3, ce qui influence probablement les résultats. C'est particulièrement vrai pour les carabes qui ont un développement holométabole, donc pour qui les traits des adultes sont très différents de ceux des immatures. Dans un tel cas, il n'est pas possible d'associer les traits de l'adulte à ses stades immatures contrairement aux autres taxa étudiés

(diplopode, isopodes, araignées et opilions) qui ont un développement amétabole. Étudier la variabilité intraspécifique des traits des arthropodes devrait être une priorité dans les prochaines années.

Assemblage des communautés

Malgré ces limitations, les résultats obtenus aident à mieux comprendre la structure des communautés et la dynamique des réseaux trophiques en permettant d'identifier des mécanismes reliant les différents niveaux trophiques entre eux. Les résultats du chapitre 3 complètent bien ceux du chapitre 2 qui permettent de mieux comprendre les mécanismes impliquer dans les interactions entre espèces. Ainsi on observe dans le chapitre 3 que les traits fonctionnels liés à l'alimentation des consommateurs sont à la fois influencés par les facteurs abiotiques et les traits de palatabilité de leurs ressources. Ensuite, les interactions réalisées entre les espèces vont résulter du couplage des traits d'alimentation des consommateurs et de palatabilité de leur ressource. Ces deux aspects sont importants pour comprendre la dynamique des réseaux trophiques (Gravel et al. 2016). La structure fonctionnelle des communautés n'est probablement pas stable dans le temps en raison des variations dans les périodes d'activités des espèces et de leur différent stade de développement, ainsi que par l'action top-down que les consommateurs peuvent avoir. Par contre, l'amplitude de ces variations est difficile à prévoir. Cet aspect serait probablement plus facile à étudier avec les décomposeurs puisque leurs ressources vont varier de façon plus linéaire que les proies des prédateurs. Leurs ressources s'accumulent rapidement à l'automne, mais l'apport en nouvelles ressources est très faible par la suite; ainsi le ratio feuilles à décomposition rapide / feuilles récalcitrantes devrait diminuer rapidement au cours de la saison, ce qui se reflète potentiellement sur les traits des espèces et des stades de développement actifs. Si tel est le cas, la taille et la force moyennes des décomposeurs devraient tendre à être plus faibles au printemps qu'à la

fin de l'été. L'échantillonnage pour le chapitre 3 a commencé à la mi-juin; mes données ne permettent donc pas de tester cette hypothèse.

L'effet top-down des prédateurs devrait varier selon la distribution des traits d'alimentation des prédateurs et de palatabilité des proies. On peut émettre l'hypothèse que si les traits d'alimentation et de palatabilié sont équitablement distribués (i.e. qu'ils présentent une dispersion fonctionnelle similaire) la pression de prédation sera équitable sur l'ensemble des proies. Dans un tel scénario, les interactions devraient être principalement determinées par la probabilité de rencontre; donc les proies les plus abondantes devraient être les plus prédatées, ce qui favoriserait une plus grande diversité spécifique en diminuant la compétitivité des espèces dominantes. Par contre, si les traits d'alimentation des prédateurs et de palatabilité des proies ne sont pas répartis équitablement (i.e. tous les prédateurs ont des pièces buccales faibles), la pression de prédation ne sera pas répartie équitablement. Dans un tel scénario, la pression de prédation devrait favoriser l'établissement des espèces à cuticule dur. De plus, les prédateurs ne joueront pas de rôle dans la compétitivité entre les espèces à cuticule dure. Ceci peut favoriser l'établissement d'une espèce dominante et diminuer la richesse spécifique (et fonctionnelle) de la communauté. Un tel scénario est plus probable dans une situation ou les filtres de dispersion ou abiotiques effectuent un tri non aléatoire sur les traits d'alimentation des prédateurs due à une corrélation entre leurs traits de dispersion ou de réponse, et leurs traits d'alimentation.

Le couplage des traits d'alimentation et de palatabilité est l'aspect le plus direct relié à la probabilité d'interaction entre les espèces, mais les aspects reliés à la probabilité de rencontre sont aussi importants (Gravel et al. 2016). Les filtres abiotiques vont avoir un impact direct sur la composition en espèce et vont tendre à uniformiser les traits de réponses dans la communauté (Cornwell et al. 2006, Grime 2006). La capacité de dispersion va également influencer la composition en espèce, particulièrement dans

les habitats isolés (e.g. par la fragmentation du paysage) ou récemment perturbés. Par contre l'impact de la dispersion sur la structure fonctionnel est probablement plus aléatoire et difficile à prévoir (Sonnier et al. 2010). Développer des traits reliés à ces filtres et voir s'ils covarient avec les traits d'alimentation est donc important.

Dans la littérature sur les traits fonctionnels des arthropodes, la capacité de dispersion est généralement considérée comme élevée ou faible et est seulement pertinente par comparaison à l'intérieur du taxon étudié. Par exemple, pour les carabes, une capacité de dispersion élevée correspond à la présence d'ailes fonctionnelles chez l'adulte (Ribera et al. 2001). Par contre, cette caractéristique ne permet pas de comparer la capacité de dispersion des carabes ailés par rapport aux autres insectes ailés. Certaines métriques permettraient une comparaison comme la portance (correspondant à la surface des ailes / la masse de l'insecte), mais sont rarement utilisées (mais voir Barton et al. 2013). De façon générale, une grande portance favorise les longs déplacements (Angelo et Slansky 1984), alors qu'une faible portance favorise la manoeuvrabilité (Chai et Srygley 1990).

Les traits reliés à la réponse aux filtres abiotiques posent un problème différent puisqu'ils dépendent d'aspect physiologique beaucoup plus difficile à étudier que la biomécanique. La seule façon efficace de procéder à ce stade-ci est par l'expérimentation; i.e. en observant espèce par espèce leur tolérance à la température ou à la perte d'humidité (Cerdá et al. 1998, Wiescher et al. 2012). Par contre, c'est une approche fastidieuse et qui demande un grand nombre de réplication (Chown 2001, Bahrndorff et al. 2006), démontrant une fois de plus l'importance de grandes bases de données accessibles.

Prédateurs et décomposition (une expérience échouée)

Au début de ma thèse, une expérience sur l'effet de la diversité fonctionnelle des prédateurs sur la vitesse de décomposition avait été proposée, mais des tests préliminaires ont rapidement démontré que l'objectif était inatteignable. L'expérience prévoyait de varier la diversité fonctionnelle des prédateurs dans des microcosmes installés en milieu naturel. Un mélange de feuilles composé de *Quercus rubra*, *Fagus grandifolia* et *Acer saccharum* en proportion égale de 3 g était installé dans quatre sacs à maille de 1 cm dans chaque microcosme. Cinq niveaux de diversité fonctionnelle étaient créés avec différentes combinaisons de trois espèces de prédateurs: *Synuchus impunctatus* (~9 mm), un Carabidae à chasse active; *Pirata montanus* (~4.5 mm), une araignée Lycosidae à chasse active; *Wadotes hybridus* (~10 mm), une araignée Agelenidae à chasse de type "sit and wait". Des microcosmes à diversité fonctionnelle élevée était également composé avec cinq espèces de prédateurs: *Carabus nemoralis* (~23 mm) et *Pterostichus coracinus* (~15 mm), deux Carabidae à chasse active; *Cicurina robusta* (~6 mm), une araignée Dictynidae à toile au sol; *Tasgius melanarius* (~15 mm), un Staphylinidae à chasse active; et *W. hybridus*. La conception des microcosmes permettait le passage des petits arthropodes grâce à des ouvertures latérales recouvertes de moustiquaire à mailles fines de 0.6 mm.

Plusieurs problèmes ont émergé de cette expérience. Malgré l'utilisation des mailles fines, plusieurs prédateurs ont réussi à s'introduire dans les microcosmes: principalement des pseudoscorpions, des petites araignées et des Staphylinidae. De plus, le taux de mortalité en un mois était assez élevé: 50 % pour *P. montanus* et 73 % pour *S. impunctatus*. Finalement, peu d'informations sont disponibles dans la littérature sur l'alimentation spécifique des prédateurs utilisés. En somme, nous n'étions pas en mesure de savoir si les proies disponibles leur convenaient et s'ils allaient vraiment pouvoir s'alimenter. L'expérience était définitivement trop

ambitieuse. Avec du recul, je considère qu'une telle expérience aurait plus de chance d'être concluante en travaillant à deux niveaux. Premièrement, il faudrait déterminer les traits effets des décomposeurs influençant la vitesse de décomposition et développer des outils permettant de prédire l'impact d'une communauté diversifiée sur la décomposition. Deuxièmement, il faudrait déterminer comment les traits effets des prédateurs influencent la structure des communautés de décomposeurs. Les connaissances actuelles ne permettent pas de répondre à l'un ou l'autre des points.

Conclusion

Au cours des 3-4 dernières années, il y a eu une amélioration marquée dans la qualité des articles publiés sur l'approche fonctionnelle avec les arthropodes, ce qui démontre que l'approche à atteint une certaine maturité grâce aux enseignements tirés des études pionnières et davantage exploratoire. En particulier, des réflexions conceptuelles ont été entamées (Pey et al. 2014b, Fountain-Jones et al. 2015) et une importance plus grande a été accordée aux traits effets (Fründ et al. 2013, Munyuli 2014, Coulis et al. 2015, Deraison et al. 2015). La prochaine étape est probablement d'établir des objectifs communs pour standardiser l'approche, particulièrement en établissant une liste de traits d'intérêt général et définir des méthodes standards de mesure pour les traits selon le modèle disponible avec les plantes (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013). L'établissement récent de bases de données de traits (Pey et al. 2014a) est un pas important vers un effort de standardisation.

La covariation entre les traits devrait être étudiée plus en profondeur, particulièrement en intégrant une plus grande variation dans les gradients de facteurs abiotiques comme l'humidité. Dans le chapitre 3, le gradient sélectionné représentait uniquement la composition spécifique des arbres; les parcelles n'ont donc pas été sélectionnées pour maximiser la variation des gradients de température et d'humidité. Avec le

développement des traits effets des arthropodes, il sera également intéressant de voir comment ces traits covarient avec les filtres abiotiques et biotiques. Finalement, certains traits effets sont difficiles à mesurer, comme ceux reliés au taux d'assimilation et les caractéristiques des fèces (Coulis et al. 2015). Par contre, il est à prévoir que ces traits effets covarient avec certains traits d'alimentation comme la taille et la densité des dents utilisés pour déchiqueter le substrat (Köhler et Alberti 1990), ce qui faciliterait leur étude à grande échelle.

ANNEXE A

ADDITIONAL NOTES ON THE LITERATURE REVIEW OF THE FUNCTIONAL TRAITS APPROACH WITH TERRESTRIAL ARTHROPODS

Table A.1 Examples of sentences identifying the hypotheses relating the filters, the function and the traits in the study of the functional traits approach with terrestrial arthropods.

	Examples	Reference
1. Filter identified	"[...] the assembly of bee pollinator communities is strongly influenced by **climatic factors** as well as **variation in food resource availability** [...]"	Ramírez et. al (2015)
	"Phytophagous beetles will respond primarily to local habitat type, reflecting their utilisation of **resources** (e.g. ruderal plant seed) that show a relatively lower degree of spatial and temporal variability compared with invertebrate prey."	Woodcock et al. (2010)
	"Native Remnants are **structurally** unique, being a **complex** and relatively low-disturbed habitat. Native Pastures are different being structurally **simple** but a relatively low-disturbed habitat. Lastly, Crop Stubble is again dissimilar, being extremely **simple** in plant diversity (one primary species – wheat), structure and habitat architecture, as well as being highly disturbed."	Yates & Andrew (2011)
	"As decreasing sand dynamics result in **deeper soil development** and **higher nutrient availability** [...]. In addition, as sand stabilization results in a more **buffered microclimate** [...]"	Bonte et al. (2006)
	"[...] mites would be affected indirectly because Dimilin interferes with chitin synthesis of their food or prey, fungi and insects."	Prinzing et al. (2002)
	"In apple orchards, the disturbances are a complex result of pesticides usages with direct (lethal) and indirect (**depletion of preys**) effects"	Mazzia et al. (2015)
	"As the chemical composition and morphological **characteristics of living leaves are transferred in leaf litter**, this in turn influences the structure and composition of the soil biota community, which thrives on litter as a source of nutrients and energy. For instance, leaf thickness and area-to-volume ratio affect organism colonization patterns and animals' **ability to ingest litter as food** [...]"	Santorufo et al. (2015)

2. Relating function to filters	"Specifically, we expected a high disturbance tolerance in species [...] (iii) which **feed** on fresh macrophyte detritus, rather than fungal microphytes, because Dimilin **negatively effects many fungi** by inhibiting their Chitin biosynthesis and thereby indirectly **increases the availability of undecomposed macrophyte detritus**" (filter = available resource; function = diet)	Prinzing et al. (2002)
	"Emerging work on bees and butterflies has demonstrated that the effects of **habitat loss and isolation** on taxonomic diversity depend strongly on the expression of traits related to **dispersal ability** and feeding breadth." (filter = habitat loss and isolation; function = dispersal ability)	Perović et al. (2015)
	"High **concentrations of metals in leaf litter** or in certain microorganisms negatively affect the collembolan community, causing shifts in their **food habits** and/or in their habitats" (filter = food digestibility; function = food habits)	Santorufo et al. (2015)
	"We predicted that insect responses would be associated with their **dispersal ability**, with specialist species having wing morphologies that enable the rapid location of new carrion resources." (filter = presence of ephemeral resource; function = dispersal ability)	Barton et al (2013)
3. Relating traits to function	"In **reproduction mode**, we were interested in an amount of sexual vs. parthenogenetic species. Parthenogenesis is generally assumed to **facilitate establishment** of populations and fast recovery after disturbance. On the other hand, sexual species were reported to **be fast colonizers**."	Farská et al. (2014)
	"The same can be said for the Femur length; species travelling short distances to reach food or shelter having shorter legs."	Yates & Andrew (2011)
	"**diet**: 1 = extremely microphytophagous due to **minute and elongated mouth parts**, 2 = microomnivorous, **mouthparts suitable for a wide dietary range** [...]"	Prinzing et al. (2002)
	"Migratory tendency was strongly correlated with traits reflecting dispersal ability [...]"	Perović et al. (2015)
	"**Relative leg length** — Longer legs allow **faster** and **more efficient locomotion** and **foraging**, but also increase their crosssectional area, which could prevent them from utilizing some foraging niches and types of shelter. Thus, relative leg length might yield information about **the mode of resource acquisition**."	Bihn et al. (2010)

Table A.2 Synthesis of the principal functional traits found in the terrestrial arthropod literature and relation to their hypothesized function. Functions were grouped in relation to their link with dispersal, abiotic and biotic ecological filters or associated ecosystem processes. Body size was kept apart as it is related to the three categories. Traits for which the function was not described in reviewed literature were put at the end of the table. Numbers beside taxa refer to the reference list. For each function, traits are ordered based on their commonness in the literature. In many cases, the link between the trait and the function is purely hypothetical. Type represent: M= Morphology, P= Physiology, L = Life history, B= Behaviour and F=Feeding.

Function	Traits	Type	Taxa
Dispersal ability, abiotic interaction, biotic interaction	Body size*	M, F	Multi-taxa: 3-5, 7, 9 Acari: 23, 25-27 Araneae: 10-15, 30-36 Collembola: 23, 38-43 Hemiptera: 15 Orthoptera: 34, 44-46, 48 Carabidae: 10, 11, 13, 15-18, 51-54, 56-65 Coccinellidae: 70, 74 Scarabaeidae: 71 Coleoptera: 14, 19, 66, 68-69, 73, 75 Lepidoptera: 77, 81, 82, 84-89 Apoidea: 18, 20, 21, 93, 94, 97-99 Formicidae: 19, 100-106, 109-113 Syrphidae: 114-116
Dispersal			
Aerial dispersal	Presence/ absence of wings	M	Multi-taxa: 7 Orthoptera: 44, 45 Hemiptera: 15, 50 Carabidae: 10-13, 15, 17, 18, 51-57, 59-65 Coleoptera: 14, 66, 72, 73
	Ballooning	B	Araneae: 10-13, 15, 28, 31, 33, 36
	Migratory status	B	Lepidoptera: 88-90

Function	Traits	Type	Taxa
			Syrphidae: 114-116
	Dispersal range	M+B	Lepidoptera: 76-79, 81, 83
	Aerial activity level	B	Multi-taxa: 2, 5, 6 Carabidae: 63
Foraging distance	Inter-tegular distance*	M	Apoidea: 21, 92, 93, 97-99
	Mobility	M+B	Orthoptera: 44 Coleoptera: 75 Lepidoptera: 17
	Wing loading	M, Bio	Coleoptera: 19
	Wing shape	M	Lepidoptera: 84
Energy allocated to dispersal	Wing length	M	Orthoptera: 46 Lepidoptera: 17, 87, 89
Ground dispersal	Appendage and eye development	M	Collembola: 39
	Walking activity level	B	Multi-taxa: 2
Foraging speed	Femoral length	M	Araneae: 32 Carabidae: 16, 51, 57 Formicidae: 100-103, 105, 106, 109-113
	Length of whole leg	M	Collembola: 40-42 Coleoptera: 69 Formicidae: 103
Climbing ability	Tarsal length	M	Carabidae: 16, 51, 57 Formicidae: 109
Vertical movement	Femoral width	M	Carabidae: 16, 51, 57
	Metatrochanter length	M	Carabidae: 51
Hydrochory	Hydrochory	B	Orthoptera: 44
Abiotic filters			
Habitat used	Position of nest	B	Scarabaeidae: 71 Apoidea: 18, 92-94, 97-98 Formicidae: 107, 112
Habitat structure	Head width*	M	Carabidae: 57

Function	Traits	Type	Taxa
			Coleoptera: 69 Formicidae: 101, 103, 106, 109, 113
	Eye position	M	Formicidae: 101, 106, 109, 110, 113
	Body width	M	Acari: 25 Araneae: 35
Vertical distribution	Number of eyes	M	Collembola: 38, 40-42
	Trichobothria	M	Collembola: 40-42
	Life form	M	Collembola: 16
Microhabitat	Number of claws	M	Acari: 25, 27
	Claw length	M	Acari: 25
	Flattened body	M	Araneae: 31
	Notogaster length	M	Acari: 25
	Sensillus length	M	Acari: 25
Habitat complexity	Tibial length	M	Araneae: 35 Carabidae: 16 Formicidae: 101, 109
Resistance and tolerance			
Desiccation resistance	Oviposition place*	B	Multi-taxa: 9 Orthoptera: 44, 48
	Pilosity	M	Carabidae: 16, 58 Formicidae: 113
	Surface structure	M	Acari: 27
	Hair length	M	Formicidae: 109
	Sclerotisation level	M	Araneae: 31
	Water loss rate	P	Formicidae: 103
Protection against UV	Body pigmentation	M	Collembola: 38, 40-43
Flood tolerance	Respiration system	M	Syrphidae: 114-116
Survival to temporary difficult conditions	Diapause	L	Multi-taxa: 9 Lepidoptera: 86
Survival to fire	Borrowing behavior	B	Araneae: 31

Function	Traits	Type	Taxa
Temperature tolerance	Foraging thermal limit	P	Formicidae: 103
Biotic filters			
Competition			
Phenology	Overwintering stage	L	Araneae: 36 Hemiptera: 50 Carabidae: 17, 51, 52, 58, 60, 61, 63, 65 Lepidoptera: 17, 81, 82, 85-88, 90 Syrphidae: 114, 116
	Foraging period*	L	Multi-taxa: 9 Araneae: 15, 28, 30 Hemiptera: 15 Carabidae: 13, 15, 17, 51, 52, 58 Coleoptera: 68 Apoidea: 92, 96 Syrphidae: 115, 116
	Activity period length	L	Araneae: 13, 31, 34 Carabidae: 13, 63 Coleoptera: 68 Lepidoptera: 77, 81, 86, 87 Apoidea: 92, 97
	Breeding season*	L	Carabidae: 13, 17, 51, 52, 56, 58, 60, 62 Syrphidae: 114
	Hatching period	L	Orthoptera: 45 Carabidae: 58
	Adult emergence period	L	Carabidae: 51, 52
	Activity period (immature)	L	Carabidae: 59
	Pupation period	L	Lepidoptera: 85
	Time for female to be mature after adult emergence	L	Lepidoptera: 86
Fecundity	Voltinism	L	Multi-taxa: 9 Hemiptera: 50

Function	Traits	Type	Taxa
			Coccinellidae: 70, 74 Lepidoptera: 17, 80, 82, 83, 85-88 Apoidea: 92 Syrphidae: 114-116
	Sexual vs. parthenogenesis	L	Acari: 22, 23 Collembola: 22, 23, 39-43
	Number of ovarioles	M	Orthoptera: 44, 48 Lepidoptera: 86
	Number of eggs	L	Multi-taxa: 9 Lepidoptera: 17, 87
	Fecundity	L	Multi-taxa: 9
	Number of brood	L	Apoidea: 18
	Number of ripe eggs	L	Lepidoptera: 86
	r/K strategy	L	Lepidoptera: 78
Niche separation	Circadian activity*	B	Multi-taxa: 3 Araneae: 12 Carabidae: 12, 14, 17, 51, 52, 58, 60 Scarabaeidae: 71 Coleoptera: 68 Formicidae: 103-105
Growth rate of the population	Time to adult stage	L	Araneae: 31 Syrphidae: 114-116
	Life cycle length	L	Acari: 24 Carabidae: 52, 60
	Generation time	L	Acari: 24
	Larval growth rate	L	Lepidoptera: 86
	Maternal care	B	Araneae: 36
	Number of larval stages	L	Orthoptera: 48
Resource characteristics			
Toughness	Head width*	M, F	Carabidae: 57 Coleoptera: 69 Formicidae: 101, 103, 106, 109, 113

Function	Traits	Type	Taxa
	Mandible width	M, F	Orthoptera: 48 Formicidae: 101, 113
	Head length	M, F	Formicidae: 101, 103, 109
Size	Tongue/ proboscis length*	M, F	Apoidea: 92, 94, 99 Pollinators (general): 20
	Mandible length	M, F	Formicidae: 101, 109-110, 113
	Chelicerae size	M, F	Araneae: 32
	Mandibular gape	M, F	Formicidae: 101
	Proboscis diameter	M, F	Pollinators (general): 20
Movement speed of prey	Fang length	M, F	Araneae: 35
Defense mechanism			
Predator avoidance	Jumping apparatus	M	Collembola: 23, 38, 40-43
	Scales	M	Collembola: 38, 40-42
	Oviposition place*	B	Multi-taxa: 9 Orthoptera: 44, 48
	Endophyte, endoparasite	B	Multi-taxa: 5, 9
Chemical defense	Pseudocelli	M	Collembola: 40-42
Physical defense	Spine number or length	M	Formicidae: 109, 111, 113
Sound defense			Carabidae: 63
Resource localization	Eye size*	M	Carabidae: 16, 51, 57 Formicidae: 100, 101, 105, 109, 111-113
	Antennae length*	M	Collembola: 38, 40-42 Carabidae: 16, 51, 57, 69 Formicidae: 109
Resource used (feeding)	Clypeus length	M, F	Formicidae: 101
	Mandible type	M, F	Collembola: 43
	Number of maxillary palpal segment	M, F	Formicidae: 109
Prey encountered	Hunting strategy*	B, F	Multi-taxa: 5 Araneae: 11-15, 31, 32, 34
	Shape of legs	M	Carabidae: 52, 60

Function	Traits	Type	Taxa
	Web architecture	B, F	Araneae: 14
Part of plant used	Sucking/chewing	M, F	Multi-taxa: 5
Trophic level	$^{15}N/^{14}N$	P	Formicidae: 100
Type of plant used	Mandibular morphology	M, F	Orthoptera: 45
Resource used (non-feeding)	Cleptoparasitism and social parasitism	B	Apoidea: 92, 94 Formicidae: 112
	Nest rent or self excavated	B	Apoidea: 93, 97
	Inquilinism	B	Formicidae: 114
	Material used for the nest	B	Formicidae: 108
	Slavers	B	Formicidae: 112
Effect traits			
Efficiency			
Decomposition rate	Body size*	M	Multi-taxa: 1, 8
	Assimilation efficiency	P	Multi-taxa: 8
	Consumption rate	P	Multi-taxa: 8
Foraging	Inter-tegular distance*	M	Apoidea: 18
	Leg size*	M	Carabidae: 18
	Number of flowers visited per minute	B	Apoidea: 96
	Optimal temperature	P	Apoidea: 95
Feeding rate	Body size*	M	Carabidae: 18 Orthoptera: 47, 49
Pollination speed	Time spent per flower	B	Apoidea: 96 Pollinators (general): 21
Ingestion rate	Stoichiometry (C:N ratio)	P	Orthoptera: 49
Resource partitioning			
Prey type	Circadian activity*	B	Multi-taxa: 2 Carabidae: 18
	Hunting strategy*	B	Multi-taxa: 2 Araneae: 29

Function	Traits	Type	Taxa
	Activity period*	L	Multi-taxa: 2
	Antenna length*	M	Carabidae: 18
	Breeding period*	L	Carabidae: 18
	Eye size*	M	Carabidae: 18
Visited flowers	Body size*	M	Apoidea: 91, 96
	Foraging period*	L	Apoidea: 18
	Tongue length*	M, F	Apoidea: 96
Plants used	Incisive strength	M, F	Orthoptera: 47, 49
	Molar strength	M, F	Orthoptera: 47
Niche separation	Circadian activity*	B	Apoidea: 91
Microbial activity	Feces hygroscopicity	P	Multi-taxa: 8
	Feces particle size	P	Multi-taxa: 8
	Feces surface area	P	Multi-taxa: 8
Size of ingested particles	Density of teeth on pectinate lamellae	M, F	Diplopoda: 37
Way of crushing particles	Characteristic of molar plate	M, F	Diplopoda: 37
Function undescribed			
Morphometries	Body depth	M	Pollinators (general): 21
Pronotum	Pronotum height	M	Carabidae: 16, 51, 57
	Pronotum length	M	Carabidae: 16 Coleoptera: 69
	Pronotum width	M	Carabidae: 51, 57 Coleoptera: 69
Abdomen	Abdomen length	M	Coleoptera: 69
	Abdomen width	M	Coleoptera: 69
	Petiole width	M	Formicidae: 101
	Petiole length	M	Formicidae: 101
	Petiole height	M	Formicidae: 101
Antennae	Scape length	M	Formicidae: 101, 109, 113

Function	Traits	Type	Taxa
Wings	Elytra width	M	Carabidae: 16, 51
	Elytra length	M	Carabidae: 16
Legs	Tibial length	M	Orthoptera: 48
Structures	Pteromorphae	M	Acari: 27
	Seta type	M	Acari: 27
	Antennal organ	M	Collembola: 38
	Number of teeth on pectinate lamellae	M	Diplopoda: 37
	Molar tuft [Y/N]	M	Diplopoda: 37
	Number of teeth on mandibles	M	Formicidae: 109
	Pollen collection organ	M	Apoidea: 92 Pollinators (general): 21
	Post antennal organ	M	Collembola: 38, 40-43
	Number of vesicles per post antennal organ	M	Collembola: 42
	Number of labial palpal segments	M	Formicidae: 109
Color	Body color	M	Carabidae: 16-17, 51 Formicidae: 105, 111
	Leg color	M	Carabidae: 16, 51
	Melanic form present	M	Coccinellidae: 70, 74
Sociality	Level of sociality	M	Apoidea: 18, 92-94, 97, 98 Pollinators (general): 21
	Immature solitary/ gregarious	B	Multi-taxa: 9
	Nymph with or without cocoon (?)	M	Formicidae: 108
Shape	Body shape	M	Collembola: 40-42
	Shape of dentes	M	Collembola: 38
	Shape of the pronotum	M	Carabidae: 51
Behavior	Overwintering place	B	Lepidoptera: 85

* This trait is associated with more than one function in the table

Multi-taxa

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Araneae & Coleoptera

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ANNEXE B

SPECIES TRAIT VALUES

Table B.1 Average trait values of ground beetle (Carabidae) species used in a feeding experiment. When multiple individuals were measured, the standard deviation is given. Details on trait measurements are provided in Annexe C.

Species	Body Length (mm)	Strength (N)	Gape (mm)	Eye size (mm)	Mandibles			
					Length (mm)	Terebra length (mm)	Absorp. length (mm)	Apical teeth (mm)
Nebria (Boreonebria) lacustris Casey, 1913 (2♀)	9.8±0.4	0.54	1.1±0.4	0.09±0.01	1.24±0.05	0.57	0.13	0.14±0.05
Notiophilus aeneus (Herbst, 1806) (1♂)	5.5	0.5	0.55	0.28	0.65	0.25	0	0.05
Carabus (Archicarabus) nemoralis Müller, 1764 (2♀, 2♂)	24.8±1.5	1.05±0.03	3.7±0.2	0.04±0.01	3.15±0.15	1.4±0.15	1.13±0.06	0.39±0.08
Bembidion (Pseudoperyphus) chalceum Dejean, 1831 (1♀)	5	0.34	0.52	0.12	0.6	0.25	0.03	0.05
Elaphropus anceps (LeConte, 1848) (1♂)	2.1	0.16	0.27	0.07	0.24	0.12	0	0.04
Myas cyanescens Dejean, 1828 (2♀, 1♂)	14.5±0.5	0.54±0.13	1.95±0.1	0.07±0.02	1.86±0.41	0.75±0.03	0.23±0.05	0.1±0.04
Pterostichus (Bothriopterus) mutus (Say, 1823) (1♀)	13	0.73	1.43	0.03	1.4	0.7	0.18	0.1

Species	Body Length (mm)	Strength (N)	Gape (mm)	Eye size (mm)	Mandibles			
					Length (mm)	Terebra length (mm)	Absorp. length (mm)	Apical teeth (mm)
Pterostichus (Monoferonia) diligendus (Chaudoir, 1868) (2♀)	11.5±0.3	0.59	1.6±0.04	0.02	1.7	0.8±0.04	0.21±0.04	0.18±0.07
Pterostichus (Euferonia) coracinus (Newman, 1838) (4♀, 1♂)	13.3±1.6	0.85±0.14	1.81±0.17	0.14±0.02	1.85±0.16	0.92±0.14	0.26±0.08	0.23±0.02
Pterostichus (Euferonia) lachrymosus (Newman, 1838) (1♂)	16	0.78	2.1	0.02	2.15	1.1	0.17	0.3
Pterostichus (Lamenius) caudicalis (Say, 1823) (1♂)	11.3	0.71	1.43	0.04	1.55	0.73	0.1	0.18
Pterostichus (Cylindrocharis) rostratus (Newman, 1838) (1♀, 1♂)	15.5±0.7	0.88±0.09	2.6±0.14	0.01	3±0.07	1.4±0.21	0.19±0.01	0.23±0.04
Pterostichus (Hypherpes) tristis (Dejean, 1828) (3♀, 1♂)	11.7±1	0.7±0.06	1.56±0.1	0.04±0.01	1.62±0.1	0.76±0.07	0.14±0.02	0.17±0.03
Anisodactylus (Anisodactylus) harrisii LeConte, 1863 (1♂)	11.3	1.09	1.23	0.02	1.43	0.43	0.4	0.3
Harpalus (Euharpalops) providens Casey, 1914 (1♂)	13	1.4	0.75	0.09	1.7	0.5	0.47	0.43
Synuchus (Pristodactyla) impunctatus (Say, 1823) (1♂)	9.5	0.46	1.13	0.02	1	0.53	0.09	0.1
Agonum (Europhilus) retractum LeConte, 1846 (1♂)	6.9	0.51	0.6	0.04	0.68	0.3	0.05	0.04

Species	Body Length (mm)	Strength (N)	Gape (mm)	Eye size (mm)	Mandibles			
					Length (mm)	Terebra length (mm)	Absorp. length (mm)	Apical teeth (mm)
Platynus (Platynus) opaculus (LeConte, 1863) (1♀)	12	0.41	1.13	0.21	1.13	0.53	0.1	0.13
Platynus (Platynus) tenuicollis (LeConte, 1846) (1♀, 1♂)	9.3±0.6	0.42±0.03	1.08±0.07	0.14±0.06	1.03±0.14	0.5±0.04	0.09±0.01	0.1
Perigona nigriceps (Dejean, 1831) (1♀, 1♂)	2.8±0.0	0.14±0.0	0.3±0.0	0.13±0.0	0.33±0.0	0.19±0.0	0	0.03

Table B.2 Trait values of the prey used in the feeding experiment. The range of values is given and the number of measured specimens are shown in [ ] when multiple individuals were measured in the experiment. Details on trait measurements are provided in Annexe C.

Phylum	Order	Family	Species	Stage*	Length (mm)	Width (mm)	Toughness (g mm^{-2})	Speed
Annelida	Haplotaxida	Enchytraeidae	Enchytraeidae sp.	U	10	0.4	0	1
		Lombricidae	Lombricidae sp. [12]	I	9 - 35	0.5 - 1.7	13	1
			Lombricidae sp. [8]	A	45 - 100	2 - 6	13	1
Mollusca	Pulmonata	"Slug"	Slug sp. 1	U	14	3.1	20	1
		"Slug"	Slug sp. 2	U	7	2.7	18	1
		"Slug"	Slug sp. 3	U	30	8	20	1
		"Slug"	Slug sp. 4	U	10	2	20	1
		"Snail"	Snail sp. 1	U	4.9	2	56	1
Platyhelminthes	Tricladida	Geoplanidae	*Microplana terrestris* (Müller, 1773)	U	12	0.9	0	1
Arthropoda	Pseudoscorpiones	Chernetidae	*Pselaphochernes scorpioides* (Hermann, 1804) [11]	I-A	0.8 - 2.4	0.3 - 0.8	0 - 14	3
	Araneae	Gnaphosidae	*Haplodrassus* sp.	A	2.8	0.9	4 - 6	3

Phylum	Order	Family	Species	Stage*	Length (mm)	Width (mm)	Toughness (g mm^{-2})	Speed
		Thomisidae	*Ozyptila* sp. [2]	I	3 - 3.5	1.4 - 1.5	6 - 12	2
		Linyphiidae	Linyphiidae sp.	A	1.2	0.6	4 - 6	3
		Lycosidae	*Pirata* sp. [5]	I	2.3 - 4.8	0.6 - 1.8	4 - 14	4
	Acariformes	Trombidiidae	Trombidiidae sp.	A	1.5	1	0	2
	Isopoda	Armadillidiidae	*Armadillidium vulgare* Latreille, 1804 [3]	I-A	1.7 - 8.5	0.7 - 5	16 - 40	3
		Porcellioniidae	*Trachelipus rathkei* (Brandt, 1833) [21]	I-A	2.5 - 10.4	0.9 - 5.2	8 - 40	3
		Trichoniscidae	*Trichoniscus pusillus* Brandt, 1833	I	2	0.9	0 - 2	3
			Hyloniscus riparius (Koch, 1838) [2]	I-A	3.2 - 3.9	1 - 1.5	3	3
	Julida	Blaniulidae	*Blaniulus guttulatus* (Fabricius, 1798)	A	7	0.4	6	2
			Choneiulus palmatus (Němec, 1895)	A	8	0.4	6	2
		Julidae	*Cylindroiulus caeruleocinctus* Wood, 1864 [4]	I-A	5 - 23	0.5 - 1.9	15 - 70	2
			Ophyiulus pilosus (Newport, 1842) [2]	A	14	1	30	2
	Polydesmida	Polydesmidae	*Polydesmus inconstans* Latzel, 1884 [2]	A	9	1.3	36 - 40	3
			Pseudopolydesmus serratus (Say, 1821)	A	25	3.3	62 - 92	3
	Spirobolida	Spirobolidae	*Narceus americanus* (de Beauvois, 1817) [4]	I	8 - 20	1 - 2	40 - 70	2
			Narceus americanus (de Beauvois, 1817) [2]	A	30 - 70	2.5 - 4.5	87 - 154	2
	Geophilomorpha	Linotaeniidae	*Strigamia chionophila* Wood, 1862 [2]	I-A	9 - 20	0.5 - 0.6	2 - 4	4
	Lithobiomorpha	Lithobiidae	Lithobiidae sp. [4]	I	5 - 8.4	0.5 - 0.9	4 - 6	4
	Entomobryomorpha	Entomobryidae	*Lepidocyrtus* sp. [2]	A	0.6 - 1	0.2 - 0.3	0	5
			Entomobryidae sp. [3]	A	2 - 3	0.5 - 0.7	0	5
	Poduromorpha	Hypogastruridae	Hypogastruridae sp. 1	A	2	0.6	0	5
Arthropoda	Symphypleona	Sminthurididae	*Sminthurides* sp.	A	0.3	0.2	0	5
	Diplura	Campodeidae	*Eumesocampa frigilis* (Hilton, 1936)	A	3	0.4	0	2
	Dermaptera	Forficulidae	*Forficula auricularia* L., 1758 [2]	I	5	1	8 - 10	3
	Hemiptera	Aphididae	Aphididae sp.	A	2	0.7	0	2
	Thysanoptera	Thripidae	*Frankliniella* sp.	A	0.8	0.2	0	2
	Pscocodea	Myopsocidae	*Lichenomima* sp. [2]	A	3	1.5	0	3
	Coleoptera	Carabidae	*Carabus nemoralis* Müller, 1764	L	25	5	28 - 34	3

Phylum	Order	Family	Species	Stage*	Length (mm)	Width (mm)	Toughness (g mm^{-2})	Speed
			Pterostichus sp. [2]	L	11 - 12	1.5 - 1.6	6 - 8	4
			Perigona nigriceps (Dejean, 1831)	A	3	1.2	16 - 20	4
		Hydrophilidae	*Anacaena limbata* (Fabricius, 1792) [2]	A	2	1	14 - 18	3
			Cymbiodyta sp. [2]	A	4.4	2.5	14 - 18	3
			Cercyon sp. [3]	A	2.5 - 3.2	1.5 - 2.1	27	3
			Cercyon sp.	L	2	0.5	0	2
			Cryptopleurum minutum (Fabricius, 1775)	A	2	1.1	20	3
		Silphidae	*Necrophila americana* (L., 1758)	L	20	6	30 - 62	3
		Staphylinidae	*Philonthus politus* (L., 1758)	A	11.2	2	38 - 58	4
			Philonthus sp. 2	A	4.5	1.1	9	4
			Philonthus sp. 3 [3]	A	5.1 - 7.9	1.1 - 1.5	20	4
			Philonthus sp. 4	A	9.1	1.9	20	4
			Staphylinidae sp. 1	A	5.4	1.1	8 - 10	4
			Staphylinidae sp. 2	A	4	1	10	4
			Staphylinidae spp. [11]	L	5 - 20	0.8 - 2	1 - 14	4
		Geotrupidae	Geotrupidae sp.	L	14	4	8	1
		Scarabaeidae	*Ataenius* sp. [3]	A	4.3	1.6	34 - 52	2
		Elmidae	*Stenelmis mera* Sanderson, 1938	A	3	1	136 - 146	2
			Stenelmis mera Sanderson, 1938 [2]	L	5 - 5.3	0.7 - 0.9	16	2
		Elateridae	Elateridae sp.	A	3.2	1	10 - 28	3
			Elateridae sp.	L	8.5	1.1	6 - 28	2
		Lampyridae	Lampyridae sp. [3]	L	8.9 - 10	1.4 - 2.5	12 - 14	2
		Cantharidae	Cantharidae sp. [5]	L	1.9 - 4.2	0.4 - 0.9	0 - 6	3
		Nitidulidae	*Epuraea rufa* (Say, 1825)	A	3.2	1.5	30 - 34	3
			Stelidota sp.	A	2.7	1.5	38 - 54	3
			Glischrochilus quadrisignatus (Say, 1835) [2]	A	5 - 5.2	1.8 - 2.3	46 - 60	3
		Cryptophagidae	*Cryptophagus* sp.	A	2.5	0.6	20 - 26	3
		Coccinellidae	Coccinellidae sp. [3]	L	6.5 - 10	1.5 - 2.6	6 - 8	3

Phylum	Order	Family	Species	Stage*	Length (mm)	Width (mm)	Toughness (g mm^{-2})	Speed
Arthropoda	Coleoptera	Mycetophagidae	*Litargus* sp.	A	1.9	0.8	20 - 26	3
		Chrysomelidae	*Labidomera clivicollis* (Kirby, 1837) [2]	L	3.8 - 4.8	2.5 - 3.8	6 - 8	2
		Curculionidae	*Sciaphilus asperatus* (Bonsdorff, 1785)	A	3	1.7	48 - 66	2
		'Unkwown'	Coleoptera sp. 1	L	2.1	0.5	0	2
			Coleoptera sp. 2	L	3	0.8	0	2
	Hymenoptera	Formicidae	Formicidae sp.	A	2.8	0.5	2 - 10	4
	Mecoptera	Panorpidae	*Panorpa* sp.	L	9	1.5	6 - 8	2
	Lepidoptera	Geometridae	Geometridae sp. 1	L	15	1.2	6 - 22	2
			Geometridae sp. 2	L	16	1.3	6 - 22	2
		Erebidae	*Hypena* sp. [2]	L	13 - 19	1.1 - 2	6 - 22	2
			Euchaetes egle (Drury, 1773)	L	20	4.5	12 - 22	2
			Spilosoma sp.	L	40	5	12 - 22	2
			Orgyia leucostigma (Smith, 1797)	L	25	5	12 - 22	2
		Psychidae	*Psyche* sp. [3]	L	2 - 4.8	0.6 - 1.5	4 - 26	2
		Notodontidae	Notodontidae sp.	L	10	3	2 - 8	2
		'Unkwown'	Lepidoptera sp. 1 [3]	L	4.1 - 11	0.7 - 1.4	0 - 22	2
			Lepidoptera sp. 2	L	5	1	2 - 8	2
			Lepidoptera sp. 3	L	10	1.5	2 - 8	2
			Lepidoptera sp. 4	L	12	1.5	6 - 22	2
			Lepidoptera sp. 5	L	12.5	1.1	6 - 22	2
			Lepidoptera sp. 6	L	14	2	6 - 22	2
			Lepidoptera sp. 7	L	9.1	2	2 - 8	2
			Lepidoptera sp. 8	L	3.5	0.5	0 - 4	2
	Diptera	Limoniidae	Limoniidae sp. [10]	L	2.9 - 11	0.3 - 1.8	0 - 12	1
		Tipulidae	Tipulidae sp. [14]	L	6 - 30	0.6 - 2.5	8 - 22	1
		Ceratopogonidae	Ceratopogonidae sp. [4]	L	2.5 - 2.9	0.2 - 0.3	0	1
		Cecidomyiidae	Cecidomyiidae sp. [2]	L	1.7 - 2.5	0.3 -0.5	0	1
		Sciaridae	Sciaridae sp. [2]	L	3.7 - 4.5	0.3 - 0.5	2	1
		Psychodidae	Psychodidae sp.	L	2.1	0.4	0	1

Phylum	Order	Family	Species	Stage*	Length (mm)	Width (mm)	Toughness (g mm^{-2})	Speed
		Scatopsidae	Scatopsidae sp. [4]	L	1.3 - 2.3	0.3 - 0.5	0	1
		Stratiomyidae	*Microchrysa polita* (L., 1758)	L	6	1.8	8	1
			Ptecticus trivittatus (Say, 1829) [5]	L	8.2 - 11.4	3 - 4.3	8	1
		'Unknown'	Diptera sp. 1	L	5.5	1	0	1
			Diptera sp. 2	L	1.8	0.4	0	1
			Diptera sp. 3	L	6.2	0.8	0	1
			Diptera sp. 4	L	6	0.7	0	1
			Diptera sp. 5	L	3.5	1.2	0	1
			Diptera sp. 6	L	4	1	0	1
			Diptera sp. 7	L	5	0.9	0	1
			Diptera sp. 8	L	2.5	0.4	0	1
			Eggs					
Arthropoda	Acariformes	Acaridae	*Tyrophagus* sp.	E	0.1	0.1	0	0
			Collembola sp. [2]	E	0.1	0.1	0	0
			Pupa					
Arthropoda	Coleoptera	Coccinellidae	Coccinellidae sp.	P	5.1	3.2	12	0
	Hymenoptera	Formicidae	Formicidae sp.	P	2.8	1	12	0
	Lepidoptera		Lepidoptera sp. 9	P	17	5	12	0
	Diptera	Ceratopogonidae	Ceratopogonidae sp.	P	2.1	0.5	22	0
		Phoridae	*Megaselia* sp. [2]	P	2.5	0.9	22	0
			Phoridae sp. 2 [2]	P	1.7	0.5	22	0
		Scatopsidae	Scatopsidae sp. [3]	P	2.2 - 2.4	0.5 - 0.6	22	0
		'Unknown'	Diptera sp. 9	P	4.7	2	22	0
			Dead					
Annelida	Haplotaxida	Enchytraeidae	Enchytraeidae sp.	U	4.5	0.4	0	0
Arthropoda	Pseudoscorpiones	Chernetidae	*Pselaphochernes scorpioides* (Hermann, 1804)	I-A	0.8	0.3	0	0
		Neobisiidae	*Microbisium* sp.	I	1.2	0.5	0	0
	Acariformes		Oribatida sp.	A	0.4	0.2	0	0
	Parasitiformes	Parasitidae	Parasitidae sp.	A	2.7	2.7	0	0

Phylum	Order	Family	Species	Stage*	Length (mm)	Width (mm)	Toughness (g mm^{-2})	Speed
	Isopoda	Armadillidiidae	*Armadillidium vulgare* Latreille, 1804 [4]	I-A	7.9 - 8.5	4.3 - 5	40	0
		Porcellioniidae	*Trachelipus rathkei* (Brandt, 1833) [8]	I-A	3 - 9.8	1.2 - 5.2	9 - 18	0
		Trichoniscidae	*Hyloniscus riparius* (Koch, 1838)	A	5.4	2.2	4	0
	Julida	Julidae	*Cylindroiulus caeruleocinctus* Wood, 1864 [4]	I-A	8 - 20	0.9 - 1.6	23 - 70	0
		Parajulidae	*Uroblaniulus canadensis* (Newport, 1844)	I	15	1.5	72	0
	Geophilomorpha	Linotaeniidae	*Strigamia chionophila* Wood, 1862	I-A	20	0.6	4	0
	Lithobiomorpha	Lithobiidae	Lithobiidae sp.	I	7.5	0.9	4	0
	Poduromorpha	Hypogastruridae	Hypogastruridae sp. 2	A	0.5	0.1	0	0
			Hypogastruridae sp. 3 [3]	A	1.5	0.5	0	0
	Diplura	Campodeidae	*Eumesocampa frigilis* (Hilton, 1936)	A	3	0.4	0	0
	Hemiptera	Cicadellidae	*Dikrella* sp.	A	4.2	1	2	0
	Coleoptera	Carabidae	*Carabus nemoralis* Müller, 1764	L	25	5	28 - 34	0
Arthropoda	Coleoptera	Hydrophilidae	*Cercyon* sp.	L	1.7	0.4	0	0
			Cercyon sp. [2]	A	2.5 - 3.7	1.5 - 2.3	24 - 30	0
			Cryptopleurum sp. [3]	A	1.5 - 2	0.9 - 1.1	20	0
		Staphylinidae	Paederinae sp.	A	4.8	0.7	10	0
			Philonthus politus (L., 1758)	A	11.2	2	49	0
			Philonthus sp. 3 [2]	A	3.2 - 8.5	0.5 - 3.6	9-20	0
			Staphylinidae sp. [4]	L	4.3 - 14	0.5 - 1.5	1 - 6	0
		Nitidulidae	*Stelidota* sp.	A	2.7	1.5	38 - 54	0
	Diptera	Limoniidae	Limoniidae sp.	L	9	1.1	10	0
		Ceratopogonidae	Ceratopogonidae sp.	L	2.7	0.3	0	0
		Chironomidae	Chironomidae sp.	A	2.5	2	0	0
		Sciaridae	Sciaridae sp.	L	2.2	0.2	2	0
		Psychodidae	Psychodidae sp.	L	2.1	0.4	0	0
		Phoridae	Phoridae sp.	L	2	0.4	0	0
		Scatopsidae	Scatopsidae sp.	L	1.3	0.3	0	0
		Stratiomyidae	*Ptecticus trivittatus* (Say, 1829) [2]	A	10.5	2.5	0	0

Phylum	Order	Family	Species	Stage*	Length (mm)	Width (mm)	Toughness (g mm^{-2})	Speed
			Ptecticus trivittatus (Say, 1829)	L	9.5	3	8	0

* A = Adult; E = Egg; I = Immature; L = Larva; P = Pupa; U = Unsure

ANNEXE C

ADDITIONAL INFORMATION ON METHODOLOGY

C.1 Ground beetles sampling and conservation

Ground beetles were collected using visual sighting and pitfall traps. Sampled habitats included river shores, forest leaf litter and open fields. Predators were kept alone in microcosms in the laboratory and starved for 24 h prior to the feeding experiment. When a ground beetle died less than five days after its collection, and did not eat any of the offered prey, it was removed from the data. Similarly, we removed all ground beetles that were found to be parasitized by Nematomorpha, given that none of parasitized ground beetle eaten any prey offered.

C.2 Prey sampling and conservation

Prey were sampled in the field on river shores, forest leaf litter, open fields and domestic compost at least twice a week from June to September 2012. Collection techniques included visual sighting, sweep nets, and Tullgren extraction of leaf litter and domestic compost. Living prey were kept together at least 12 h in the laboratory environment before offered to ground beetles, but could have been kept as long as a week. When a prey was not eaten by the ground beetle after 48 h, it was available for a second experiment with another ground beetle. Dead prey were used only if they recently died and were still soft.

C.3 Feeding experiment

Availability of prey was dependent on what was collected in the field, and thus, was not predictable (except for some species of Diplopoda and Isopoda). For this reason, we did not have a step by step protocol to determine the order of the prey that were given to the ground beetles. However, the objective was to identify the limit in trait values with which a ground beetle species can interact. Thus, as much as possible, we started with a soft prey species that was about half the size of the ground beetle. Subsequent prey were either larger or smaller until an upper and lower limit was estimated; i.e. the ground beetles did not interact with prey of a given size for which the other traits and the phylogeny varied.

C.2 Ground beetles

C.2.1 Body size

Body size is recognized as one of the most important traits determining interactions between predators and their prey (Cohen et al. 1993, Schneider et al. 2012, Gravel et al. 2013). We measured body size as the length of the ground beetle from labrum to elytra tip (Fig. C.1). All our species of ground beetles had long elytra covering the whole abdomen. Species under 14 mm were measured with a graduated ocular and dissection microscope to a precision of 0.1 mm. Larger specimens were measured with a standard ruler to the nearest mm.

Figure C.1 Measurement of the length. Specimen = *Elaphropus anceps*.

Figure C.2 Measurement of head width. Specimen = *Synucus impunctatus*.

C.2.2 Mandibular strength

Mandibular strength constrains prey selection relative to its cuticular toughness. Mandibular strength was determined with the formula $h \times b/c$ where h was the width of the head, b was the basal width of the mandible and c its length (Wheater and Evans 1989). We measured the head width (h) just behind the eyes where muscles responsible for closing the mandibles are attached. Temples were included in the measurement when developed (as on Fig. C.2). Basal width (b) of the mandible was measured from upper condyle to the abductor muscle attachment point, while mandibular length (c) was measured from upper condyle to mandible apex (Fig. C.3). Both measurements were made on the left mandible.

Figure C.3 Measurement of the basal width of mandible (b) and mandibular length (c). Specimen = *Anisodactylus harrisii*.

Figure C.4 Measurement of mandibular gape based on labrum length (L) and length of cutting edge of the mandibles (c). Specimen = *Pterostichus adoxus*.

C.2.3 Mandibular gape

Mandibular gape constrains prey selection relative to its body size; principally body width and depth (Brodie and Formanowicz 1983, Evans and Forsythe 1985, Lawson and Morgan 1993, Brannen et al. 2005). Maximum mandibular gape depends on the length, shape and angle of attachment of the mandibles; however, we were unable to find any metric to estimate it. We observed that the blade of the mandible generally fitted with the lateral border of the labrum on dead specimens with mandibles open to their maximum. Also, generally, only the terebra (cutting edge) of the mandibles extended past the labrum. Thus, we considered that maximum mandibular gape (g) was given by:

$$g = L + 2c(\sin(\alpha))$$

where L was the length of the labrum; c was the length of the terebra of the left mandible (see section 1.5) and α was an angle in an imaginary right-angled triangle where the terebra represented the hypotenuse (Fig. C.4). The angle α was measured by opening the left mandible to the maximum. Then, a picture was taken under a dissecting microscope. On the pictures, the specimens were oriented so that the labrum appeared as flat as possible to ensure replicability between specimens. The angle was determined with the image analysis software ImageJ. As we had few specimens of each species, we used the average measured angle of all specimens to reduce measurement variability. Measured angles varied between 18° and 38° with a mean value at 28°. We considered an angle of 30° so that $sin\ (30°) = 0.5$ and $g = L + c$.

C.2.4 Eye size

Eye size of predators is related to prey detection and species feeding on fast moving prey tend to have larger eyes (Bauer & Kredler 1993). We measured eye size relative to head size by dividing the volume of one eye by the head volume. Eye volume was measured as the product between length and height from a side view, and width from a dorsal view (Fig. C.5). Head volume was measured as the product between head width behind the eyes, the length from clypeal edge to occipital suture from a dorsal view, and the height across the eye in a lateral view.

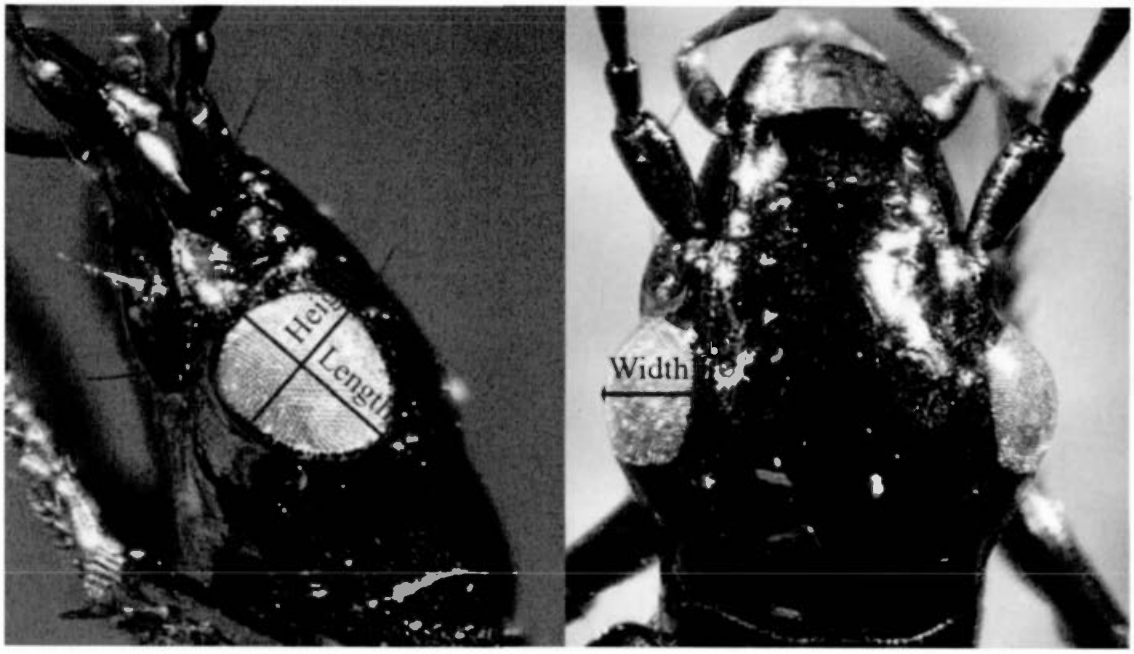

Figure C.5 Measurement of the dimension of the eye of ground beetles. Specimen = *Platynus opaculus*.

C.2.5 Mandibles

All measurements were made on the left mandible that was extracted from the head. We used the same **mandibular length** as for the mandibular strength. **Apical tooth length** was measured from the terebra to the apex on the internal dorsal side (Fig. C.6). **Absorption section length** and **terebra length** were measured from the dorsal side of the mandible (Fig. C.6).

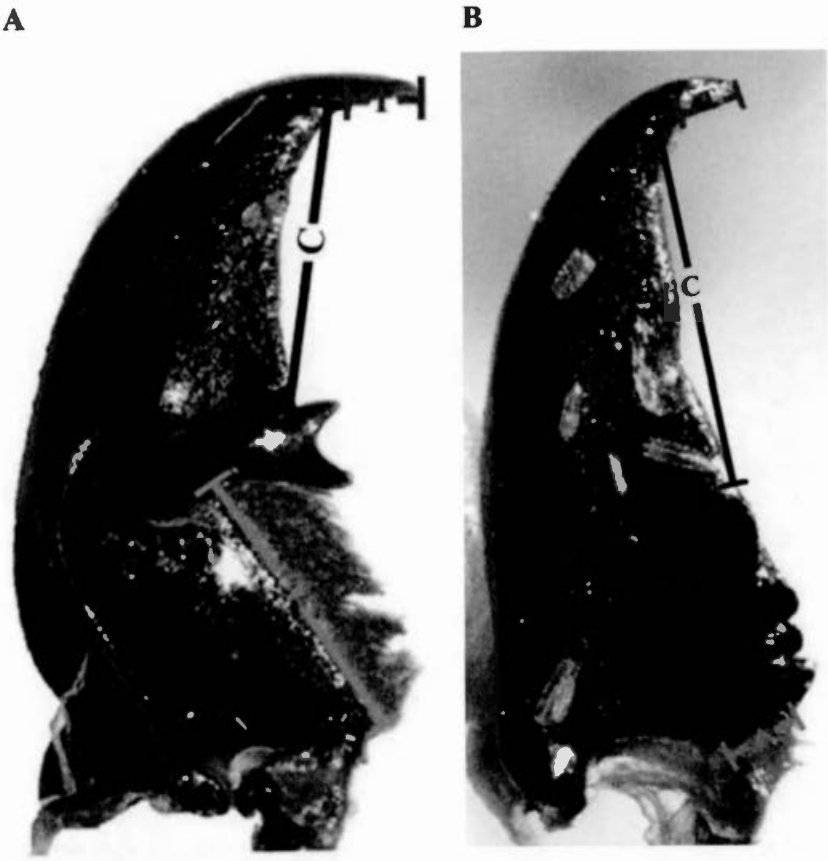

Figure C.6 Measurement of the apical tooth length (T), length of terebra (C) and length of absorption section on left mandible of A) *Carabus nemoralis*, and B) *Chlaenius emarginatus*.

C.3. Prey

C.3.1 Body size

Two body size measurements were taken on each prey type. Measurements were done on living individuals when possible. First, as for ground beetles, body length was measured from the tip of the head to the tip of the abdomen (Fig. C.7). For snails and case bearer caterpillars, the length was the longest side of their protective device.

Secondly, the width was measured as the largest portion from a dorsal view (Fig. C.7).

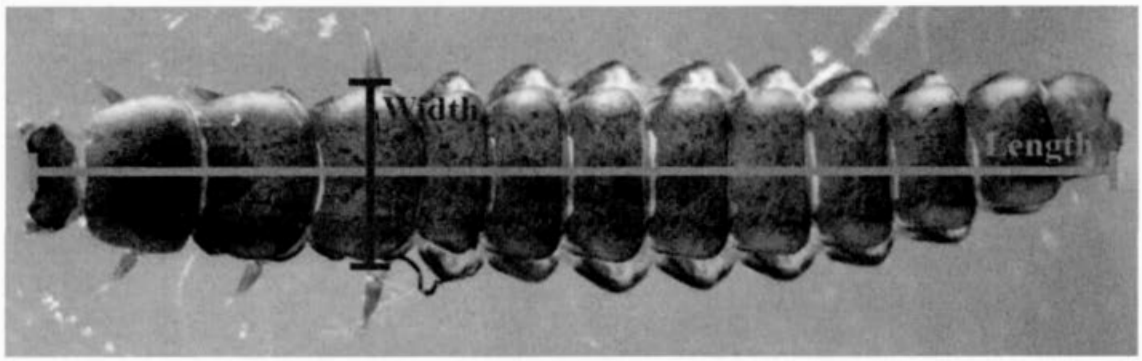

Figure C.7 Measurement of body length and width on prey. Specimen = Lampyridae sp.

C.3.2 Cuticular toughness

Cuticular toughness was measured with a Pesola® Medio-Line pressure set to which we added an entomological pin of size 2 (diameter = 0.45 mm). Toughness was the pressure required to break through the integument with the pin in g mm^{-2}. A value of zero was given for very small and soft prey. Toughness of the cuticle can be variable depending on the body part, so measurements were consistently taken at the level of the abdomen from the dorsal side. In small beetles, it was sometimes easier to take the measurement on the elytra alone. For 5 species out of 115 (4 %), we had no extra specimens to measure the toughness. In these few cases, we inferred toughness measured on very similar species. One species of snail was removed from the analysis because the shell decomposed partially in alcohol and we were unable to get a reliable measurement.

C3.3 Speed of movement

Speed of movement was estimated as a five level categorical variable determined by the presence/ absence of legs, ability to run and ability to jump (Table C.7).

Table C.7 Speed of movement categories of prey based on presence/absence of legs, ability to run and ability to jump.

Value	Type	Characteristics
0	Immobile	Egg, pupa, dead
1	Crawl	No legs
2	Walk	Short legs
3	Can run	Mid-length legs
4	Mostly runner	Long legs
5	Jump	Jumping apparatus

ANNEXE D

DETERMINING THE SMOOTH TERM IN THE GENERAL ADDITIVE MODELS (GAM)

The danger of GAM is to add too much smooth so that the curve overfits the observed data (Wood 2006, p. 128) making it ecologically meaningless. To prevent this problem, we tested separately each trait-match to find the lower smooth required to obtain an ecologically interpretable curve. The lowest possible smoothing (i.e. three) was set to the trait-match predator mandibular strength/ prey cuticular toughness as increasing the value of the smoothing did not affect the relationship (Figure D.1). A smoothing of three was also attributed to the trait-match predator eye size/ prey speed as a smoothing of five resulted in an unexpected sinusoidal relationship (Figure D.2). Conversely, a smoothing of five was set to trait-match predator size/ prey size as a smoothing of three created an unexpected sinusoidal relationship with larger prey; the sinusoidal was less marked at a smoothing of five (Figure D.3). A smoothing of five was also attributed to the trait-match predator mandibular gape/ prey body width as no relationships were predicted for larger gape values with a smoothing of three, while a smoothing of ten created a complex pattern (Figure D.4). A smoothing of three was attributed to the four unmatched traits.

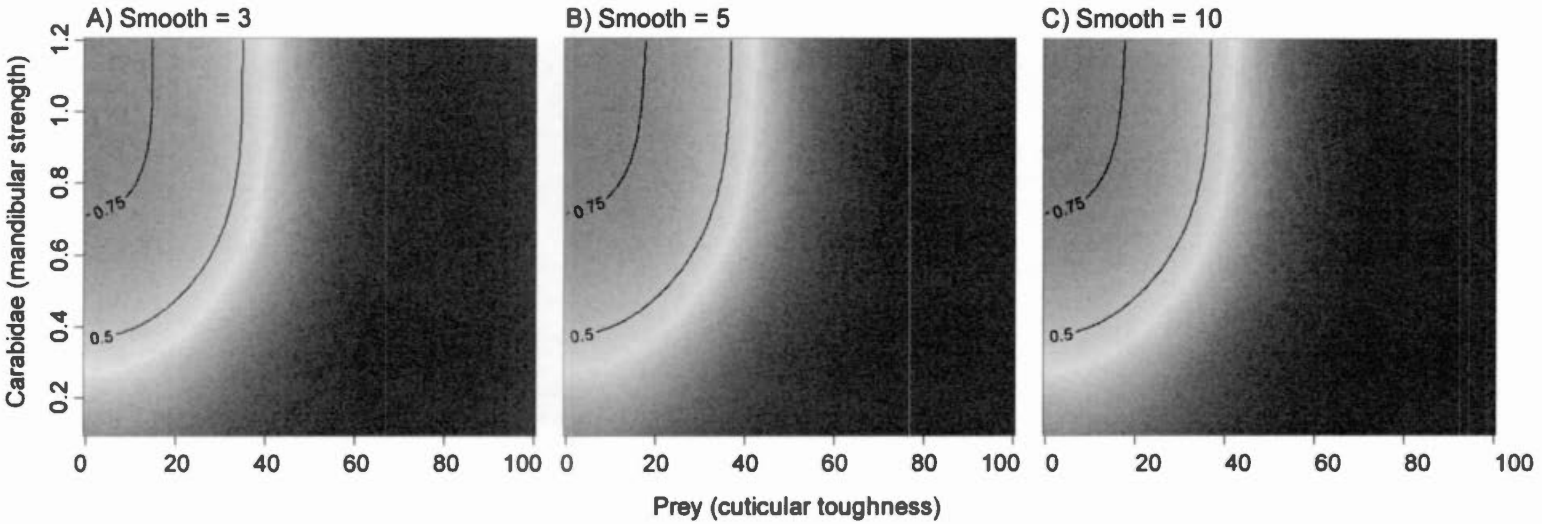

Figure D.1 Predicted probability of interaction between a Carabidae and a prey as a function of mandibular strength of the predator and the cuticular toughness of the prey based on the matching-centrality formalism in a GAM model with three different values for the smooth term. Predicted probability of interaction decreases from green to red.

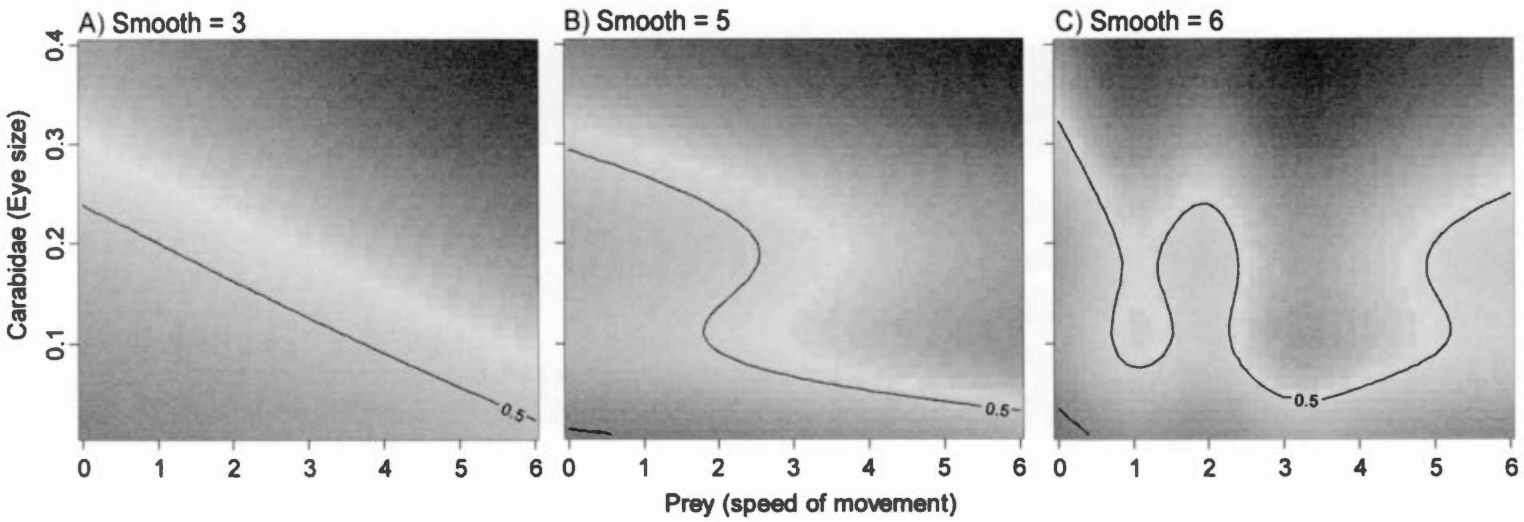

Figure D.2 Predicted probability of interaction between a Carabidae and a prey as a function of eye size of the predator and the speed of movement of the prey based on the matching-centrality formalism in a GAM model with three different values for the smooth term. Predicted probability of interaction decreases from green to red.

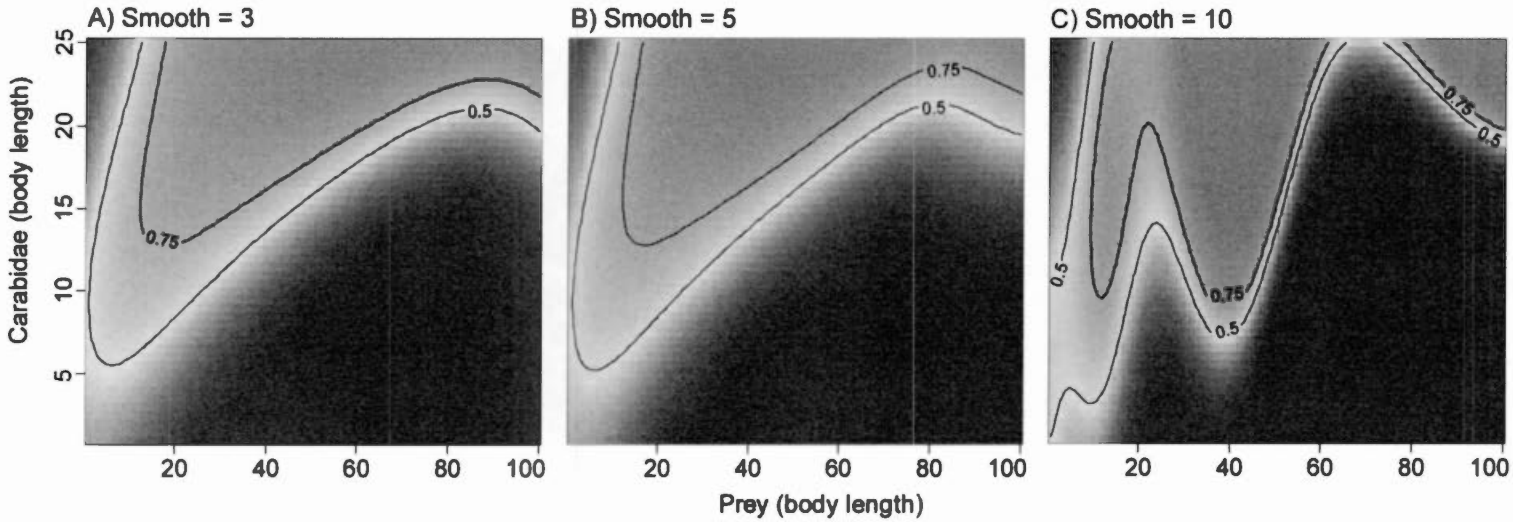

Figure D.3 Predicted probability of interaction between a Carabidae and a prey as a function of their respective body length based on the matching-centrality formalism in a GAM model with three different values for the smooth term. Predicted probability of interaction decreases from green to red.

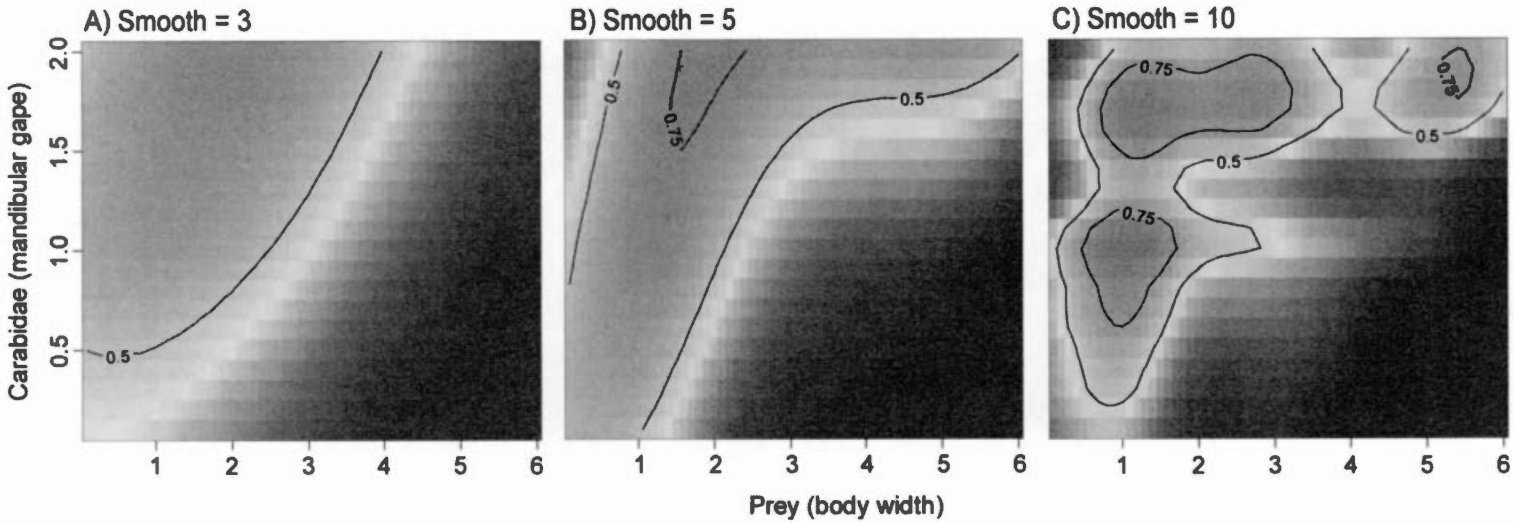

Figure D.4 Predicted Predicted probability of interaction between a Carabidae and a prey as a function of mandibular gape of the predator and the body width of the prey based on the matching-centrality formalism in a GAM model with three different values for the smooth term. Predicted probability of interaction decreases from green to red.

ANNEXE E

GOODNESS OF FIT OF THE DIFFERENT MODELS USED TO PREDICT PREDATOR/ PREY INTERACTIONS

Table E.1 Goodness of fit for all potential combinations of four trait-matches and four unmatched traits with and without a phylogenetic term. For each model, interactions between 20 Carabidae species and 115 prey species were predicted based on the matching-centrality formalism in a general additive model (GAM). Models are ordered by the true skill statistic value (TSS). Highlighted models represent the best and the most parsimonious ones.

Model*	Phyl	Accuracy	Sensitivity	Specificity	TSS
Size + Stength + Eyes + Mandible + Terebra	Yes	83.41	87.07	78.31	0.65
Size + Stength + Gape + Eyes + Terebra	Yes	82.96	88.21	75.66	0.64
Size + Stength + Gape	Yes	82.52	88.21	74.6	0.63
Size + Stength + Mandible + Absorption	Yes	82.74	88.21	75.13	0.63
Size + Stength + Terebra + Absorption	Yes	82.74	88.21	75.13	0.63
Size + Stength + Gape + Eyes	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Mandible	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Terebra	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Tooth	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Absorption	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Eyes + Mandible	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Eyes + Tooth	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Eyes + Absorption	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Mandible + Terebra	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Mandible + Tooth	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Mandible + Absorption	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Terebra + Tooth	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Terebra + Absorption	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Tooth + Absorption	Yes	82.52	88.21	74.6	0.63
Size + Stength + Mandible + Terebra + Absorption	Yes	82.74	88.21	75.13	0.63
Size + Stength + Terebra + Tooth + Absorption	Yes	82.74	88.21	75.13	0.63
Size + Stength + Gape + Eyes + Mandible + Tooth	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Eyes + Terebra + Tooth	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Eyes + Terebra + Absorption	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Eyes + Tooth + Absorption	Yes	82.52	88.21	74.6	0.63
Size + Stength + Gape + Terebra + Tooth + Absorption	Yes	82.52	88.21	74.6	0.63
Size + Stength + Eyes + Mandible + Terebra + Absorption	Yes	82.74	88.21	75.13	0.63
Size + Stength + Mandible + Terebra + Tooth + Absorption	Yes	82.74	88.21	75.13	0.63
Size+Stength+Gape+Eyes+Mandible+Terebra Tooth	Yes	82.52	88.21	74.6	0.63

Model*	Phyl	Accuracy	Sensitivity	Specificity	TSS
Size+Stength+Gape+Eyes+Mandible+Tooth+Absorption	Yes	82.52	88.21	74.6	0.63
All	Yes	82.52	88.21	74.6	0.63
Size + Stength + Eyes + Mandible	Yes	81.86	87.07	74.6	0.62
Size + Gape + Mandible + Tooth	Yes	82.08	88.59	73.02	0.62
Size + Stength + Eyes + Terebra + Absorption	Yes	82.08	87.83	74.07	0.62
Size + Gape + Eyes + Tooth + Absorption	Yes	82.52	89.35	73.02	0.62
Size + Gape + Mandible + Terebra + Absorption	Yes	82.52	89.35	73.02	0.62
Size + Stength	Yes	81.42	87.07	73.54	0.61
Size + Stength + Absorption	Yes	81.42	87.07	73.54	0.61
Size + Stength + Eyes + Absorption	Yes	81.42	87.07	73.54	0.61
Size + Stength + Mandible + Terebra	Yes	81.42	87.07	73.54	0.61
Size + Stength + Eyes + Mandible + Absorption	Yes	81.42	87.07	73.54	0.61
Size + Stength + Gape + Mandible + Tooth + Absorption	Yes	82.3	90.49	70.9	0.61
Size + Stength + Gape + Eyes + Terebra + Tooth + Absorption	Yes	81.86	88.97	71.96	0.61
Size+Stength+Gape+Mandible+Terebra + Tooth + Absorption	Yes	81.86	88.59	72.49	0.61
Size + Mandible	Yes	80.97	85.55	74.6	0.6
Size + Mandible + Terebra	Yes	80.97	85.55	74.6	0.6
Size + Stength + Tooth	Yes	80.97	87.07	72.49	0.6
Size + Stength + Eyes + Tooth	Yes	80.97	87.07	72.49	0.6
Size + Stength + Terebra + Tooth	Yes	80.97	87.07	72.49	0.6
Size + Stength + Tooth + Absorption	Yes	81.42	88.59	71.43	0.6
Size + Stength + Eyes + Terebra + Tooth	Yes	80.97	87.07	72.49	0.6
Size + Stength + Eyes + Tooth + Absorption	Yes	81.42	88.59	71.43	0.6
Size + Stength + Mandible + Terebra + Tooth	Yes	80.97	87.07	72.49	0.6
Size + Stength + Mandible + Tooth + Absorption	Yes	80.97	87.07	72.49	0.6
Size + Stength + Gape + Eyes + Mandible + Terebra	Yes	81.19	88.21	71.43	0.6
Size + Stength + Eyes + Mandible + Terebra + Tooth	Yes	81.42	88.59	71.43	0.6
Size + Stength + Eyes + Mandible + Tooth + Absorption	Yes	81.42	88.59	71.43	0.6
Size + Stength + Eyes + Terebra + Tooth + Absorption	Yes	81.42	88.59	71.43	0.6
Size+Stength+Eyes+Mandible+Terebra + Tooth + Absorption	Yes	80.97	87.07	72.49	0.6
Size + Stength + Eyes	Yes	80.53	86.69	71.96	0.59
Size + Stength + Terebra	Yes	80.53	86.69	71.96	0.59
Size + Stength + Mandible	Yes	80.97	87.83	71.43	0.59
Size + Stength + Eyes + Terebra	Yes	80.53	86.69	71.96	0.59
Stength + Gape + Eyes + Absorption	Yes	80.53	86.69	71.96	0.59
Size + Stength + Eyes + Mandible + Tooth	Yes	80.97	87.45	71.96	0.59
Stength + Gape + Mandible + Tooth + Absorption	Yes	80.53	86.69	71.96	0.59
Stength + Gape + Eyes + Mandible + Terebra + Absorption	Yes	80.53	86.69	71.96	0.59
Stength + Gape + Mandible + Terebra + Tooth + Absorption	Yes	80.53	86.69	71.96	0.59
Stength+Gape+Eyes+Mandible+Terebra + Tooth + Absorption	Yes	80.53	86.69	71.96	0.59
Stength + Gape	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Eyes	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Mandible	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Terebra	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Tooth	Yes	80.31	87.45	70.37	0.58

Model*	Phyl	Accuracy	Sensitivity	Specificity	TSS
Stength + Gape + Absorption	Yes	80.31	87.45	70.37	0.58
Size + Gape + Eyes	Yes	80.75	89.35	68.78	0.58
Size + Gape + Tooth	Yes	80.75	89.35	68.78	0.58
Size + Gape + Absorption	Yes	80.75	89.35	68.78	0.58
Gape + Eyes + Mandible + Tooth	Yes	80.09	85.93	71.96	0.58
Size + Stength + Mandible + Tooth	Yes	80.09	86.31	71.43	0.58
Stength + Gape + Eyes + Mandible	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Eyes + Terebra	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Eyes + Tooth	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Mandible + Terebra	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Mandible + Tooth	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Mandible + Absorption	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Terebra + Tooth	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Terebra + Absorption	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Tooth + Absorption	Yes	80.31	87.45	70.37	0.58
Size + Gape + Eyes + Mandible	Yes	80.75	89.35	68.78	0.58
Size + Gape + Eyes + Tooth	Yes	80.75	89.35	68.78	0.58
Size + Gape + Terebra + Tooth	Yes	80.75	89.35	68.78	0.58
Size + Gape + Eyes + Terebra	Yes	80.53	89.35	68.25	0.58
Size + Gape + Mandible + Absorption	Yes	80.53	89.35	68.25	0.58
Size + Gape + Terebra + Absorption	Yes	80.53	89.35	68.25	0.58
Size + Gape + Tooth + Absorption	Yes	80.53	89.35	68.25	0.58
Size + Gape + Eyes + Mandible + Terebra	Yes	80.75	89.35	68.78	0.58
Size + Gape + Eyes + Mandible + Absorption	Yes	80.75	89.35	68.78	0.58
Size + Gape + Eyes + Terebra + Tooth	Yes	80.53	89.35	68.25	0.58
Size + Gape + Eyes + Terebra + Absorption	Yes	80.75	89.35	68.78	0.58
Size + Gape + Mandible + Terebra + Tooth	Yes	80.75	89.35	68.78	0.58
Size + Gape + Terebra + Tooth + Absorption	Yes	80.75	89.35	68.78	0.58
Stength + Gape + Eyes + Mandible + Terebra	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Eyes + Mandible + Tooth	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Eyes + Mandible + Absorption	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Eyes + Terebra + Tooth	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Eyes + Terebra + Absorption	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Eyes + Tooth + Absorption	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Mandible + Terebra + Absorption	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Terebra + Tooth + Absorption	Yes	80.31	87.45	70.37	0.58
Size + Gape + Eyes + Mandible + Terebra + Tooth	Yes	80.53	89.35	68.25	0.58
Size + Gape + Eyes + Terebra + Tooth + Absorption	Yes	80.53	89.35	68.25	0.58
Stength + Gape + Eyes + Mandible + Terebra + Tooth	Yes	80.31	87.45	70.37	0.58
Stength + Gape + Eyes + Mandible + Tooth + Absorption	Yes	80.31	87.45	70.37	0.58
Size+Gape+Eyes + Mandible + Terebra + Tooth + Absorption	Yes	80.53	89.35	68.25	0.58
Size + Stength + Gape + Mandible + Terebra + Tooth	Yes	80.31	88.97	68.25	0.57
Size + Stength + Gape + Eyes + Mandible + Absorption	Yes	79.42	87.07	68.78	0.56
Size + Stength + Gape + Mandible + Terebra + Absorption	Yes	79.42	87.07	68.78	0.56
Size + Gape + Eyes + Mandible + Tooth + Absorption	Yes	80.09	90.49	65.61	0.56

Model*	Phyl	Accuracy	Sensitivity	Specificity	TSS
Size+Stength+Gape+Eyes + Mandible + Terebra + Absorption	Yes	79.42	87.07	68.78	0.56
Stength	Yes	78.76	84.41	70.9	0.55
Size + Eyes + Tooth	Yes	78.32	83.27	71.43	0.55
Size + Mandible + Tooth + Absorption	Yes	78.32	83.27	71.43	0.55
Size + Eyes + Mandible + Tooth	Yes	78.54	84.79	69.84	0.55
Size + Eyes + Mandible + Terebra + Absorption	Yes	78.76	85.17	69.84	0.55
Size + Eyes + Terebra + Tooth + Absorption	Yes	78.32	83.27	71.43	0.55
Stength + Gape + Mandible + Terebra + Tooth	Yes	78.54	84.79	69.84	0.55
Stength + Gape + Eyes + Terebra + Tooth + Absorption	Yes	78.54	84.79	69.84	0.55
Size + Gape	Yes	78.76	86.69	67.72	0.54
Size + Gape + Mandible	Yes	78.76	86.69	67.72	0.54
Size + Eyes + Mandible + Terebra + Tooth + Absorption	Yes	78.1	84.03	69.84	0.54
Mandible	Yes	76.99	79.47	73.54	0.53
Gape	Yes	77.43	83.27	69.31	0.53
Gape + Mandible	Yes	77.43	83.27	69.31	0.53
Gape + Tooth	Yes	77.43	83.27	69.31	0.53
Gape + Absorption	Yes	77.43	83.27	69.31	0.53
Gape + Eyes + Mandible	Yes	77.65	83.27	69.84	0.53
Gape + Eyes + Tooth	Yes	77.65	83.27	69.84	0.53
Gape + Eyes + Terebra	Yes	77.65	83.65	69.31	0.53
Gape + Mandible + Terebra	Yes	77.43	83.27	69.31	0.53
Gape + Mandible + Tooth	Yes	77.43	83.27	69.31	0.53
Gape + Mandible + Absorption	Yes	77.43	83.27	69.31	0.53
Gape + Terebra + Absorption	Yes	77.43	83.27	69.31	0.53
Gape + Tooth + Absorption	Yes	77.43	83.27	69.31	0.53
Size + Eyes + Terebra	Yes	77.88	84.41	68.78	0.53
Size + Mandible + Tooth	Yes	77.65	84.03	68.78	0.53
Size + Terebra + Tooth	Yes	77.88	84.41	68.78	0.53
Gape + Eyes + Mandible + Terebra	Yes	77.65	83.65	69.31	0.53
Gape + Eyes + Terebra + Tooth	Yes	77.65	83.65	69.31	0.53
Gape + Mandible + Terebra + Tooth	Yes	77.43	83.27	69.31	0.53
Gape + Mandible + Tooth + Absorption	Yes	77.43	83.27	69.31	0.53
Gape + Terebra + Tooth + Absorption	Yes	77.43	83.27	69.31	0.53
Size + Mandible + Terebra + Tooth	Yes	77.88	84.79	68.25	0.53
Gape + Eyes + Mandible + Terebra + Tooth	Yes	77.65	83.65	69.31	0.53
Gape + Eyes + Mandible + Terebra + Absorption	Yes	77.43	83.27	69.31	0.53
Gape + Mandible + Terebra + Tooth + Absorption	Yes	77.43	83.27	69.31	0.53
Gape + Eyes + Mandible + Terebra + Tooth + Absorption	Yes	77.65	83.65	69.31	0.53
Absorption	Yes	76.55	80.61	70.9	0.52
Size	Yes	77.43	84.03	68.25	0.52
Mandible + Tooth	Yes	76.55	78.33	74.07	0.52
Mandible + Absorption	Yes	76.55	78.33	74.07	0.52
Terebra + Tooth	Yes	76.77	79.47	73.02	0.52
Stength + Mandible	Yes	76.77	81.75	69.84	0.52
Stength + Absorption	Yes	76.77	81.75	69.84	0.52

Model*	Phyl	Accuracy	Sensitivity	Specificity	TSS
Size + Tooth	Yes	76.99	82.89	68.78	0.52
Gape + Eyes	Yes	77.21	83.27	68.78	0.52
Gape + Terebra	Yes	77.21	83.27	68.78	0.52
Size + Eyes	Yes	77.43	84.03	68.25	0.52
Size + Absorption	Yes	77.43	84.03	68.25	0.52
Stength + Eyes	Yes	77.21	83.65	68.25	0.52
Stength + Eyes + Mandible	Yes	76.77	81.75	69.84	0.52
Stength + Eyes + Terebra	Yes	76.77	81.75	69.84	0.52
Stength + Eyes + Tooth	Yes	76.77	81.75	69.84	0.52
Stength + Eyes + Absorption	Yes	76.77	81.75	69.84	0.52
Stength + Mandible + Terebra	Yes	76.77	81.75	69.84	0.52
Stength + Mandible + Tooth	Yes	76.77	81.75	69.84	0.52
Stength + Terebra + Tooth	Yes	76.77	81.75	69.84	0.52
Stength + Terebra + Absorption	Yes	76.77	81.75	69.84	0.52
Stength + Tooth + Absorption	Yes	76.77	81.75	69.84	0.52
Size + Tooth + Absorption	Yes	76.99	82.89	68.78	0.52
Gape + Terebra + Tooth	Yes	77.21	83.27	68.78	0.52
Size + Eyes + Mandible	Yes	77.43	84.03	68.25	0.52
Size + Eyes + Absorption	Yes	77.43	84.03	68.25	0.52
Size + Mandible + Absorption	Yes	77.43	84.03	68.25	0.52
Size + Terebra + Absorption	Yes	77.43	84.03	68.25	0.52
Stength + Eyes + Mandible + Terebra	Yes	76.77	81.75	69.84	0.52
Stength + Mandible + Terebra + Absorption	Yes	76.77	81.75	69.84	0.52
Size + Eyes + Terebra + Tooth	Yes	77.21	82.89	69.31	0.52
Size + Eyes + Tooth + Absorption	Yes	77.21	83.27	68.78	0.52
Gape + Mandible + Terebra + Absorption	Yes	77.21	83.27	68.78	0.52
Size + Eyes + Mandible + Terebra	Yes	77.43	84.03	68.25	0.52
Size + Eyes + Terebra + Absorption	Yes	77.43	84.03	68.25	0.52
Size + Mandible + Terebra + Absorption	Yes	77.43	84.03	68.25	0.52
Stength + Eyes + Mandible + Absorption	Yes	77.21	83.65	68.25	0.52
Stength + Mandible + Terebra + Tooth	Yes	77.21	83.65	68.25	0.52
Stength + Mandible + Tooth + Absorption	Yes	77.21	83.65	68.25	0.52
Size + Gape + Eyes + Absorption	Yes	77.88	86.31	66.14	0.52
Size + Gape + Eyes + Mandible + Tooth	Yes	77.65	85.93	66.14	0.52
Size + Eyes + Mandible + Terebra + Tooth	Yes	77.21	82.89	69.31	0.52
Size + Eyes + Mandible + Tooth + Absorption	Yes	77.21	82.89	69.31	0.52
Size + Mandible + Terebra + Tooth + Absorption	Yes	76.99	82.89	68.78	0.52
Stength + Eyes + Mandible + Terebra + Tooth	Yes	77.21	83.65	68.25	0.52
Stength + Eyes + Mandible + Terebra + Absorption	Yes	76.77	81.75	69.84	0.52
Stength + Eyes + Mandible + Tooth + Absorption	Yes	76.77	81.75	69.84	0.52
Stength + Eyes + Terebra + Tooth + Absorption	Yes	76.77	81.75	69.84	0.52
Stength + Mandible + Terebra + Tooth + Absorption	Yes	77.21	83.65	68.25	0.52
Stength + Eyes + Mandible + Terebra + Tooth + Absorption	Yes	77.21	83.65	68.25	0.52
Stength + Terebra	Yes	76.55	81.75	69.31	0.51
Stength + Tooth	Yes	76.55	81.75	69.31	0.51

Model*	Phyl	Accuracy	Sensitivity	Specificity	TSS
Stength + Mandible + Absorption	Yes	76.55	81.75	69.31	0.51
Size + Gape + Terebra	Yes	77.43	86.31	65.08	0.51
Stength + Eyes + Mandible + Tooth	Yes	76.55	81.75	69.31	0.51
Stength + Eyes + Terebra + Tooth	Yes	76.55	81.75	69.31	0.51
Stength + Eyes + Terebra + Absorption	Yes	76.55	81.75	69.31	0.51
Stength + Eyes + Tooth + Absorption	Yes	76.55	81.75	69.31	0.51
Stength + Terebra + Tooth + Absorption	Yes	76.55	81.75	69.31	0.51
Gape + Eyes + Tooth + Absorption	Yes	76.77	83.27	67.72	0.51
Size + Gape + Mandible + Terebra	Yes	77.43	86.31	65.08	0.51
Size + Gape + Mandible + Tooth + Absorption	Yes	77.43	86.31	65.08	0.51
Gape + Eyes + Mandible + Tooth + Absorption	Yes	76.77	83.27	67.72	0.51
Gape + Eyes + Terebra + Tooth + Absorption	Yes	76.77	83.27	67.72	0.51
Size + Gape + Eyes + Mandible + Terebra + Absorption	Yes	77.43	86.31	65.08	0.51
Size + Gape + Mandible + Terebra + Tooth + Absorption	Yes	77.21	85.93	65.08	0.51
Tooth	Yes	75.88	80.61	69.31	0.5
Tooth + Absorption	Yes	75.88	80.61	69.31	0.5
Mandible + Terebra + Tooth	Yes	75.66	79.85	69.84	0.5
Terebra + Tooth + Absorption	Yes	75.88	80.61	69.31	0.5
Mandible + Terebra + Absorption	Yes	75.88	80.99	68.78	0.5
Eyes + Terebra + Tooth + Absorption	Yes	75.66	79.85	69.84	0.5
Mandible + Terebra + Tooth + Absorption	Yes	75.66	79.85	69.84	0.5
Size + Eyes + Mandible + Absorption	Yes	76.55	85.17	64.55	0.5
Terebra	Yes	75.22	79.85	68.78	0.49
Eyes + Absorption	Yes	75.22	79.85	68.78	0.49
Mandible + Terebra	Yes	75.22	79.85	68.78	0.49
Terebra + Absorption	Yes	75.22	79.85	68.78	0.49
Eyes + Tooth + Absorption	Yes	75.44	79.47	69.84	0.49
Eyes + Mandible + Terebra + Tooth + Absorption	Yes	75.44	80.99	67.72	0.49
Eyes	Yes	74.78	79.47	68.25	0.48
Eyes + Terebra	Yes	75.22	80.23	68.25	0.48
Eyes + Mandible	Yes	74.78	79.85	67.72	0.48
Size + Terebra	Yes	75.66	85.17	62.43	0.48
Eyes + Mandible + Terebra	Yes	75.22	80.23	68.25	0.48
Eyes + Terebra + Absorption	Yes	75.22	80.23	68.25	0.48
Mandible + Tooth + Absorption	Yes	75	79.85	68.25	0.48
Gape + Eyes + Absorption	Yes	74.78	79.85	67.72	0.48
Eyes + Mandible + Absorption	Yes	74.78	79.85	67.72	0.48
Eyes + Terebra + Tooth	Yes	75	81.37	66.14	0.48
Eyes + Mandible + Terebra + Tooth	Yes	74.78	79.47	68.25	0.48
Eyes + Mandible + Terebra + Absorption	Yes	75.22	80.23	68.25	0.48
Gape + Eyes + Mandible + Absorption	Yes	74.78	79.85	67.72	0.48
Gape + Eyes + Terebra + Absorption	Yes	74.78	79.85	67.72	0.48
Eyes + Mandible + Tooth + Absorption	Yes	75	80.61	67.2	0.48
Size + Terebra + Tooth + Absorption	Yes	75.66	85.17	62.43	0.48
Eyes + Tooth	Yes	74.56	79.09	68.25	0.47

Model*	Phyl	Accuracy	Sensitivity	Specificity	TSS
Eyes + Mandible + Tooth	Yes	74.56	79.09	68.25	0.47
Phylo	Yes	73.89	77.95	68.25	0.46
Size + Stength + Gape + Eyes + Mandible	No	75.88	90.11	56.08	0.46
Size + Stength + Gape + Eyes + Tooth	No	75.66	88.59	57.67	0.46
Size + Stength + Eyes + Mandible + Tooth	No	75.88	89.73	56.61	0.46
Size + Stength + Eyes + Terebra + Tooth	No	75.88	90.49	55.56	0.46
Size + Stength + Eyes + Mandible + Terebra + Tooth	No	75.88	89.73	56.61	0.46
Size + Stength + Eyes + Mandible + Tooth + Absorption	No	75.88	89.73	56.61	0.46
Size + Stength + Gape + Eyes + Mandible + Tooth + Absorption	No	75.88	90.87	55.03	0.46
Size + Stength + Eyes + Mandible + Terebra + Tooth + Absorption	No	75.88	89.73	56.61	0.46
All	No	75.66	88.59	57.67	0.46
Size + Stength + Eyes	No	75.44	90.49	54.5	0.45
Size + Stength + Eyes + Tooth	No	75.44	90.11	55.03	0.45
Size + Stength + Eyes + Mandible	No	75.44	90.49	54.5	0.45
Size + Stength + Eyes + Absorption	No	75.44	90.49	54.5	0.45
Size + Stength + Eyes + Mandible + Terebra	No	75.44	90.49	54.5	0.45
Size + Stength + Eyes + Mandible + Absorption	No	75.44	90.49	54.5	0.45
Size + Stength + Eyes + Terebra + Absorption	No	75.44	90.49	54.5	0.45
Size + Stength + Eyes + Tooth + Absorption	No	75.44	90.11	55.03	0.45
Size + Stength + Gape + Eyes + Mandible + Tooth	No	75.88	92.02	53.44	0.45
Size + Stength + Gape + Eyes + Tooth + Absorption	No	75.88	92.02	53.44	0.45
Size + Stength + Eyes + Mandible + Terebra + Absorption	No	75.44	90.49	54.5	0.45
Size + Stength + Eyes + Terebra + Tooth + Absorption	No	75.44	90.11	55.03	0.45
Size + Stength + Gape + Eyes + Mandible + Terebra + Tooth	No	75.66	91.63	53.44	0.45
Size + Stength	No	75	91.25	52.38	0.44
Size + Stength + Terebra	No	75.22	92.02	51.85	0.44
Size + Stength + Gape + Tooth	No	75.22	91.25	52.91	0.44
Size + Stength + Mandible + Terebra	No	75	91.25	52.38	0.44
Size + Stength + Mandible + Absorption	No	75	91.25	52.38	0.44
Size + Stength + Gape + Mandible + Tooth	No	75.22	91.25	52.91	0.44
Size + Stength + Mandible + Terebra + Absorption	No	75	91.25	52.38	0.44
Stength + Gape + Eyes + Terebra + Tooth	No	75	89.73	54.5	0.44
Stength + Gape + Eyes + Tooth + Absorption	No	75	89.73	54.5	0.44
Size + Stength + Gape + Terebra + Tooth + Absorption	No	75.22	91.25	52.91	0.44
Size + Stength + Gape + Eyes + Terebra + Tooth + Absorption	No	74.78	89.35	54.5	0.44
Size + Stength + Gape + Mandible + Terebra + Tooth + Absorption	No	75.22	91.25	52.91	0.44
Stength+Gape+Eyes+Mandible+Terebra+Tooth+Absorption	No	75	89.73	54.5	0.44
Size + Stength + Gape + Eyes	No	74.34	89.35	53.44	0.43
Stength + Gape + Terebra + Tooth	No	74.56	90.11	52.91	0.43
Stength + Gape + Tooth + Absorption	No	74.56	90.11	52.91	0.43
Size + Stength + Gape + Tooth + Absorption	No	74.56	90.87	51.85	0.43
Size + Stength + Gape + Eyes + Terebra + Tooth	No	74.56	88.97	54.5	0.43
Stength + Gape + Eyes + Mandible + Terebra + Tooth	No	74.34	88.59	54.5	0.43

Model*	Phyl	Accuracy	Sensitivity	Specificity	TSS
Size+Stength+Gape+Eyes+Mandible+Terebra + Absorption	No	74.34	88.97	53.97	0.43
Stength + Eyes	No	73.23	85.17	56.61	0.42
Stength + Eyes + Mandible	No	73.45	85.55	56.61	0.42
Stength + Eyes + Terebra	No	73.23	85.17	56.61	0.42
Stength + Eyes + Absorption	No	73.23	85.17	56.61	0.42
Stength + Gape + Eyes	No	74.12	89.35	52.91	0.42
Size + Stength + Tooth	No	74.12	90.87	50.79	0.42
Stength + Eyes + Mandible + Terebra	No	73.45	85.55	56.61	0.42
Stength + Eyes + Mandible + Tooth	No	73.23	85.17	56.61	0.42
Stength + Eyes + Mandible + Absorption	No	73.45	85.55	56.61	0.42
Stength + Eyes + Terebra + Absorption	No	73.23	85.17	56.61	0.42
Stength + Gape + Eyes + Tooth	No	73.89	88.59	53.44	0.42
Size + Stength + Eyes + Terebra	No	74.12	89.35	52.91	0.42
Stength + Gape + Eyes + Mandible	No	74.12	89.35	52.91	0.42
Stength + Gape + Eyes + Terebra	No	74.12	89.35	52.91	0.42
Stength + Gape + Eyes + Absorption	No	74.12	89.35	52.91	0.42
Size + Stength + Mandible + Tooth	No	74.12	90.87	50.79	0.42
Size + Stength + Terebra + Tooth	No	74.12	90.87	50.79	0.42
Size + Stength + Tooth + Absorption	No	74.12	90.87	50.79	0.42
Size + Stength + Gape + Eyes + Terebra	No	74.12	89.73	52.38	0.42
Size + Stength + Gape + Eyes + Absorption	No	74.12	89.73	52.38	0.42
Size + Stength + Gape + Terebra + Tooth	No	74.34	90.87	51.32	0.42
Size + Stength + Mandible + Terebra + Tooth	No	74.12	90.87	50.79	0.42
Size + Stength + Mandible + Tooth + Absorption	No	74.12	90.87	50.79	0.42
Size + Stength + Terebra + Tooth + Absorption	No	74.12	90.87	50.79	0.42
Stength + Gape + Eyes + Mandible + Terebra	No	74.12	89.35	52.91	0.42
Stength + Gape + Eyes + Mandible + Tooth	No	74.34	90.87	51.32	0.42
Stength + Gape + Eyes + Mandible + Absorption	No	74.12	89.35	52.91	0.42
Stength + Gape + Eyes + Terebra + Absorption	No	74.12	89.35	52.91	0.42
Stength + Gape + Mandible + Tooth + Absorption	No	74.12	89.35	52.91	0.42
Stength + Eyes + Mandible + Terebra + Tooth	No	73.23	85.17	56.61	0.42
Stength + Eyes + Mandible + Terebra + Absorption	No	73.45	85.55	56.61	0.42
Stength + Eyes + Mandible + Tooth + Absorption	No	73.23	85.17	56.61	0.42
Size + Stength + Gape + Eyes + Mandible + Terebra	No	74.12	89.73	52.38	0.42
Size + Stength + Gape + Eyes + Mandible + Absorption	No	74.12	89.73	52.38	0.42
Size + Stength + Gape + Eyes + Terebra + Absorption	No	74.12	89.73	52.38	0.42
Size + Stength + Gape + Mandible + Terebra + Tooth	No	74.34	90.87	51.32	0.42
Size + Stength + Gape + Mandible + Tooth + Absorption	No	74.12	89.73	52.38	0.42
Size + Stength + Mandible + Terebra + Tooth + Absorption	No	74.12	90.87	50.79	0.42
Stength + Gape + Eyes + Mandible + Terebra + Absorption	No	74.12	89.35	52.91	0.42
Stength + Gape + Eyes + Mandible + Tooth + Absorption	No	73.89	88.59	53.44	0.42
Stength + Gape + Eyes + Terebra + Tooth + Absorption	No	73.89	88.59	53.44	0.42
Stength+Gape+Mandible+Terebra + Tooth + Absorption	No	74.12	89.35	52.91	0.42
Stength+Eyes + Mandible + Terebra + Tooth + Absorption	No	73.23	85.17	56.61	0.42
Stength + Mandible + Tooth	No	73.23	87.83	52.91	0.41

Model*	Phyl	Accuracy	Sensitivity	Specificity	TSS
Stength + Eyes + Terebra + Tooth	No	73.01	85.17	56.08	0.41
Stength + Eyes + Tooth + Absorption	No	73.23	85.93	55.56	0.41
Stength + Mandible + Terebra + Tooth	No	73.23	87.83	52.91	0.41
Stength + Mandible + Tooth + Absorption	No	73.23	87.83	52.91	0.41
Size + Stength + Gape + Mandible	No	73.45	89.73	50.79	0.41
Size + Stength + Gape + Terebra	No	73.45	89.73	50.79	0.41
Size + Stength + Gape + Absorption	No	73.45	89.73	50.79	0.41
Size + Stength + Gape + Mandible + Terebra	No	73.45	89.73	50.79	0.41
Size + Stength + Gape + Mandible + Absorption	No	73.45	89.73	50.79	0.41
Size + Stength + Gape + Terebra + Absorption	No	73.45	89.73	50.79	0.41
Stength + Mandible + Terebra + Tooth + Absorption	No	73.23	87.83	52.91	0.41
Size + Stength + Gape + Mandible + Terebra + Absorption	No	73.45	89.73	50.79	0.41
Stength + Eyes + Tooth	No	72.79	85.93	54.5	0.4
Size + Stength + Gape	No	73.23	89.73	50.26	0.4
Size + Stength + Mandible	No	73.67	91.25	49.21	0.4
Size + Stength + Absorption	No	73.67	91.25	49.21	0.4
Stength + Gape + Terebra + Absorption	No	72.79	87.07	52.91	0.4
Size + Stength + Terebra + Absorption	No	73.45	90.87	49.21	0.4
Stength + Gape + Mandible + Terebra + Absorption	No	72.79	87.07	52.91	0.4
Stength + Gape + Terebra + Tooth + Absorption	No	73.23	89.73	50.26	0.4
Stength + Eyes + Terebra + Tooth + Absorption	No	72.12	83.27	56.61	0.4
Stength + Terebra + Tooth	No	72.12	86.69	51.85	0.39
Stength + Tooth + Absorption	No	72.57	87.45	51.85	0.39
Stength + Terebra + Tooth + Absorption	No	72.12	86.69	51.85	0.39
Stength + Gape + Mandible + Absorption	No	73.01	89.73	49.74	0.39
Stength + Tooth	No	71.9	86.69	51.32	0.38
Stength + Gape	No	72.57	90.11	48.15	0.38
Stength + Gape + Mandible	No	72.57	90.11	48.15	0.38
Stength + Gape + Terebra	No	72.57	90.11	48.15	0.38
Stength + Gape + Absorption	No	72.57	90.11	48.15	0.38
Stength + Gape + Tooth	No	72.79	90.87	47.62	0.38
Stength + Gape + Mandible + Terebra	No	72.57	90.11	48.15	0.38
Stength + Gape + Mandible + Tooth	No	72.79	90.87	47.62	0.38
Size + Gape + Eyes + Terebra + Absorption	No	72.79	93.16	44.44	0.38
Stength + Gape + Mandible + Terebra + Tooth	No	72.79	90.87	47.62	0.38
Size + Gape + Eyes + Mandible + Terebra + Absorption	No	72.79	93.16	44.44	0.38
Stength	No	71.46	87.45	49.21	0.37
Stength + Absorption	No	71.68	86.69	50.79	0.37
Stength + Mandible	No	71.46	86.69	50.26	0.37
Stength + Terebra	No	71.46	86.69	50.26	0.37
Stength + Mandible + Terebra	No	71.46	86.69	50.26	0.37
Stength + Mandible + Absorption	No	71.46	86.69	50.26	0.37
Stength + Terebra + Absorption	No	71.46	86.69	50.26	0.37
Stength + Mandible + Terebra + Absorption	No	71.46	86.69	50.26	0.37
Size + Eyes + Mandible + Terebra + Tooth	No	72.57	93.16	43.92	0.37

Model*	Phyl	Accuracy	Sensitivity	Specificity	TSS
Size + Eyes + Mandible + Terebra + Tooth + Absorption	No	72.35	92.78	43.92	0.37
Size + Gape + Eyes + Terebra + Tooth	No	71.9	91.25	44.97	0.36
Size + Eyes + Mandible + Tooth + Absorption	No	72.12	92.78	43.39	0.36
Size+Gape+Eyes+Mandible+Terebra+Tooth + Absorption	No	71.9	91.25	44.97	0.36
Size + Eyes + Tooth	No	71.68	93.54	41.27	0.35
Size + Eyes + Mandible + Tooth	No	71.68	93.54	41.27	0.35
Size + Eyes + Terebra + Tooth	No	71.68	93.54	41.27	0.35
Size + Eyes + Mandible + Terebra + Absorption	No	71.68	93.92	40.74	0.35
Size + Gape + Eyes + Terebra	No	70.8	90.11	43.92	0.34
Size + Gape + Eyes + Tooth	No	70.8	90.11	43.92	0.34
Gape + Eyes + Mandible + Tooth	No	71.02	90.87	43.39	0.34
Gape + Eyes + Tooth + Absorption	No	70.8	90.49	43.39	0.34
Gape + Eyes + Mandible + Tooth + Absorption	No	71.02	91.63	42.33	0.34
Size + Gape + Eyes + Mandible + Tooth + Absorption	No	70.8	90.11	43.92	0.34
Gape + Eyes + Terebra	No	70.35	90.11	42.86	0.33
Gape + Eyes + Mandible + Terebra	No	70.35	89.35	43.92	0.33
Gape + Eyes + Terebra + Tooth	No	70.35	89.73	43.39	0.33
Size + Gape + Mandible + Terebra + Tooth	No	70.35	90.87	41.8	0.33
Gape + Eyes + Mandible + Terebra + Tooth	No	70.35	89.73	43.39	0.33
Gape + Eyes + Terebra + Tooth + Absorption	No	70.35	89.73	43.39	0.33
Gape + Eyes + Mandible + Terebra + Tooth + Absorption	No	70.35	89.73	43.39	0.33
Size + Tooth	No	70.8	95.44	36.51	0.32
Size + Mandible + Tooth	No	70.8	95.44	36.51	0.32
Size + Terebra + Tooth	No	70.8	95.44	36.51	0.32
Size + Tooth + Absorption	No	70.8	95.44	36.51	0.32
Gape + Eyes + Terebra + Absorption	No	69.91	89.35	42.86	0.32
Size + Mandible + Terebra + Tooth	No	69.69	89.73	41.8	0.32
Size + Terebra + Tooth + Absorption	No	70.8	95.44	36.51	0.32
Size + Eyes	No	70.13	93.54	37.57	0.31
Size + Gape + Terebra	No	69.47	90.49	40.21	0.31
Size + Gape + Tooth	No	69.91	91.25	40.21	0.31
Size + Eyes + Mandible	No	70.13	93.54	37.57	0.31
Size + Eyes + Absorption	No	70.13	93.54	37.57	0.31
Size + Gape + Mandible + Terebra	No	69.47	90.49	40.21	0.31
Size + Gape + Mandible + Tooth	No	69.91	91.25	40.21	0.31
Size + Gape + Tooth + Absorption	No	69.91	91.25	40.21	0.31
Gape + Mandible + Tooth + Absorption	No	69.69	91.25	39.68	0.31
Size + Eyes + Mandible + Absorption	No	70.13	93.54	37.57	0.31
Size + Eyes + Terebra + Absorption	No	70.35	93.92	37.57	0.31
Size + Gape + Eyes + Mandible + Terebra	No	70.13	93.54	37.57	0.31
Gape + Eyes + Mandible + Terebra + Absorption	No	69.47	89.35	41.8	0.31
Size + Gape + Eyes + Terebra + Tooth + Absorption	No	69.47	90.87	39.68	0.31
Size + Mandible	No	70.35	96.58	33.86	0.3
Size + Absorption	No	70.35	96.58	33.86	0.3
Gape + Terebra + Absorption	No	69.03	88.97	41.27	0.3

Model*	Phyl	Accuracy	Sensitivity	Specificity	TSS
Size + Gape + Absorption	No	69.47	91.63	38.62	0.3
Gape + Tooth + Absorption	No	69.25	91.25	38.62	0.3
Size + Eyes + Terebra	No	69.69	93.16	37.04	0.3
Size + Terebra + Absorption	No	70.13	95.82	34.39	0.3
Size + Mandible + Terebra	No	70.35	96.58	33.86	0.3
Size + Gape + Terebra + Absorption	No	69.25	91.25	38.62	0.3
Size + Gape + Eyes + Mandible + Tooth	No	69.03	89.73	40.21	0.3
Size + Gape + Eyes + Mandible + Terebra + Tooth	No	69.03	89.73	40.21	0.3
Gape + Terebra	No	68.58	88.59	40.74	0.29
Gape + Mandible + Terebra	No	68.36	87.83	41.27	0.29
Size + Gape + Eyes	No	68.81	89.73	39.68	0.29
Gape + Terebra + Tooth	No	68.81	89.73	39.68	0.29
Gape + Mandible + Terebra + Absorption	No	68.36	87.83	41.27	0.29
Size + Gape + Eyes + Absorption	No	68.81	89.73	39.68	0.29
Gape + Mandible + Terebra + Tooth	No	68.81	89.73	39.68	0.29
Gape + Terebra + Tooth + Absorption	No	68.81	89.73	39.68	0.29
Size + Gape + Mandible + Absorption	No	68.81	91.25	37.57	0.29
Size + Gape + Terebra + Tooth	No	69.25	92.4	37.04	0.29
Size + Mandible + Terebra + Absorption	No	69.25	92.78	36.51	0.29
Size + Gape + Eyes + Mandible + Absorption	No	68.58	88.97	40.21	0.29
Size + Gape + Mandible + Tooth + Absorption	No	69.03	92.78	35.98	0.29
Size + Gape + Terebra + Tooth + Absorption	No	69.03	92.4	36.51	0.29
Gape + Mandible + Terebra + Tooth + Absorption	No	68.81	89.73	39.68	0.29
Size + Gape + Mandible + Terebra + Tooth + Absorption	No	69.03	92.4	36.51	0.29
Gape + Eyes + Mandible	No	68.58	92.02	35.98	0.28
Gape + Eyes + Mandible + Absorption	No	68.58	92.02	35.98	0.28
Size + Gape + Eyes + Tooth + Absorption	No	68.58	91.25	37.04	0.28
Size + Eyes + Terebra + Tooth + Absorption	No	68.58	92.4	35.45	0.28
Eyes + Tooth	No	66.59	82.13	44.97	0.27
Eyes + Terebra	No	67.26	85.93	41.27	0.27
Gape + Eyes	No	67.7	90.11	36.51	0.27
Eyes + Mandible + Tooth	No	66.59	82.13	44.97	0.27
Eyes + Terebra + Tooth	No	66.59	82.13	44.97	0.27
Eyes + Tooth + Absorption	No	66.59	82.13	44.97	0.27
Eyes + Terebra + Absorption	No	67.26	85.93	41.27	0.27
Gape + Eyes + Tooth	No	67.7	89.35	37.57	0.27
Gape + Eyes + Absorption	No	67.7	90.11	36.51	0.27
Eyes + Mandible + Tooth + Absorption	No	66.59	82.13	44.97	0.27
Eyes + Terebra + Tooth + Absorption	No	66.59	82.13	44.97	0.27
Size + Mandible + Terebra + Tooth + Absorption	No	68.36	93.92	32.8	0.27
Eyes + Mandible + Terebra + Tooth + Absorption	No	66.81	82.89	44.44	0.27
Gape	No	67.48	89.35	37.04	0.26
Eyes + Mandible	No	67.04	87.07	39.15	0.26
Size + Gape	No	67.7	92.02	33.86	0.26
Eyes + Mandible + Terebra	No	67.04	87.07	39.15	0.26

Model*	Phyl	Accuracy	Sensitivity	Specificity	TSS
Eyes + Mandible + Absorption	No	67.04	87.07	39.15	0.26
Size + Gape + Mandible	No	67.7	91.63	34.39	0.26
Size + Mandible + Absorption	No	67.92	93.54	32.28	0.26
Eyes + Mandible + Terebra + Absorption	No	67.04	87.07	39.15	0.26
Size + Mandible + Tooth + Absorption	No	68.14	94.3	31.75	0.26
Size + Gape + Mandible + Terebra + Absorption	No	67.7	91.63	34.39	0.26
Eyes + Absorption	No	67.04	88.97	36.51	0.25
Gape + Mandible	No	66.81	88.97	35.98	0.25
Size + Terebra	No	67.92	95.06	30.16	0.25
Gape + Mandible + Absorption	No	66.81	88.97	35.98	0.25
Size + Gape + Eyes + Mandible	No	67.04	89.73	35.45	0.25
Size + Eyes + Tooth + Absorption	No	67.26	91.25	33.86	0.25
Gape + Tooth	No	66.59	90.49	33.33	0.24
Gape + Mandible + Tooth	No	66.59	90.49	33.33	0.24
Size + Eyes + Mandible + Terebra	No	66.81	92.02	31.75	0.24
Size	No	66.37	92.4	30.16	0.23
Gape + Absorption	No	66.37	91.63	31.22	0.23
Eyes + Mandible + Terebra + Tooth	No	63.5	74.52	48.15	0.23
Mandible + Tooth	No	63.27	74.14	48.15	0.22
Terebra + Tooth	No	63.27	74.14	48.15	0.22
Tooth + Absorption	No	63.27	74.14	48.15	0.22
Mandible + Terebra + Tooth	No	63.27	74.14	48.15	0.22
Mandible + Tooth + Absorption	No	63.27	74.14	48.15	0.22
Terebra + Tooth + Absorption	No	63.27	74.14	48.15	0.22
Mandible + Terebra + Tooth + Absorption	No	63.27	74.14	48.15	0.22
Mandible	No	63.5	80.99	39.15	0.2
Tooth	No	63.5	81.75	38.1	0.2
Mandible + Terebra	No	63.5	80.99	39.15	0.2
Mandible + Absorption	No	63.5	80.99	39.15	0.2
Terebra + Absorption	No	64.6	87.83	32.28	0.2
Mandible + Terebra + Absorption	No	63.5	80.99	39.15	0.2
Terebra	No	63.05	82.51	35.98	0.18
Absorption	No	63.94	93.92	22.22	0.16
Eyes	No	59.73	84.41	25.4	0.1

*** Trait-matches**

Size = predator body length/ prey body length
Strength = predator mandibular strength/ prey cuticular toughness
Gape = predator mandibular gape/ prey body width
Eyes = predator eye size/ prey speed movement

Unmatched traits

Mandible = predator mandible length
Absorption = Length of the liquid absorption section of predator mandible
Terebra = Length of the terebra (cutting section) of predator mandible
Tooth = Length of the apical tooth of predator mandible

APPENDICE A

FIRST RECORD IN CANADA OF *ONTHOPHILUS PLURICOSTATUS* LECONTE (COLEOPTERA: HISTERIDAE) AND A NEW MENTION FOR THE RARE SPECIES *LORDITHON NIGER* (GRAVENHORST) (COLEOPTERA: STAPHYLINIDAE)

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We report the first record of the species *Onthophilus pluricostatus* LeConte (Coleoptera: Histeridae) in Canada, and a new mention for the rare species *Lordithon niger* (Gravenhorst) (Coleoptera: Staphylinidae). One specimen of *O. pluricostatus* was caught in a pitfall trap in a red oak (*Quercus rubra* L.) stand in the Parc national du Mont-Saint-Bruno (45°33'03.5"N 73°19'27.8"W) in southern Quebec. The trap used a solution of 40% ethanol and 5% vinegar as preservative and was active during 1–23 August 2011.

Our record represents the northernmost record for *O. pluricostatus*. Its previously reported range extended northwards to Massachusetts, with the southern limit occurring in northern Florida and the western limit in Michigan (Bousquet and Laplante 2006). Although the species has not been reported from Ontario, a specimen

reported from Detroit, Michigan indicates it may be found in that province (Helava 1977, Bousquet and Laplante 2006).

Two specimens of *L. niger* were observed together (one collected) under the bark of a mid-fallen dead deciduous tree (most likely sugar maple (*Acer saccharum* Marshall) or red oak) on 18 May 2013 also in the Parc national du Mont-Saint-Bruno. The species is considered potentially endangered in New England (McCollough 1997), and potentially extirpated in Pennsylvania (Rawlins and Bier 1998) and Virginia (Roble 2003). The status of this species is unknown in Canada, but seems less critical. Campbell (1982) reports only seven records of *L. niger* after 1942, but four of these were in Quebec. Furthermore, Webster et al. (2012) report four records in New Brunswick between 2006-2009 and one in Quebec for Saint-Raphaël in 2006. The other records of this species in Quebec were for Quebec City (four records) and West Brome (Campbell 1982).

The identification of *O. pluricostatus* was confirmed by Serge Laplante from the Canadian National Collection of Insects, Arachnids and Nematodes in Ottawa, Ontario where the voucher is kept. The specimens of *L. niger* were identified by the first author and the voucher is kept in the arthropod collection in the laboratory of I. Tanya Handa at the Université du Québec à Montréal.

APPENDICE B

CONTRIBUTION À LA CONNAISSANCE DE LA DIVERSITÉ DES ARTHROPODES DU SOL DU QUÉBEC

Étudier la faune du sol m'a amené à m'intéresser à des groupes d'arthropodes qui ont été peu étudiés au Québec précédemment comme les Diplopoda et les Opiliones. Ma thèse à donc comme contribution secondaire d'augmenter nos connaissances sur la diversité de ces groupes au Québec.

J'ai identifié 18 espèces d'Opiliones durant mon piégeage; de ce nombre, quatre seraient nouvelles pour le Québec, dont une nouvelle pour le Canada (Holmberg 2007). La nouvelle espèce canadienne est *Trogulus tricarinatus* (Linné) (Trogulidae), une espèce introduite d'Europe et retrouvée précédemment dans les États de New York et du Massachusetts (Shear 2016). Un total de 15 spécimens a été capturé, tout au Mont St-Hilaire. Les trois autres nouvelles espèces pour le Québec sont *Crosbycus dasycnemus* (Crosby) (Ceratolasmatidae), *Rilaena triangularis* (Herbst) (Phalangiidae) et *Leiobunum aldrichi* (Weed) (Sclerosomatidae). Deux autres espèces potentiellement nouvelles ont également été identifiées, mais leur identification est plus incertaine et va devoir être examinée par un spécialiste: *Lacinius* sp. (Phalangiidae) et *Leiobunum exilipes* (Wood) (Sclerosomatidae).

Un total de 17 espèces de Diplopoda ont été capturées durant mon piégeage; de ce nombre, cinq sont des nouvelles mentions pour le Québec, dont une espèce probablement nouvelle pour l'Amérique du Nord. Deux autres espèces ont été trouvées lors de la recherche de proies pour les Carabidae dans le chapitre 2: trois spécimens de *Choneiulus palmatus* (Nemec) ont été collectés dans de la litière en milieu semi-humide à Laval; un spécimen de *Polydesmus denticulatus* Koch a été trouvé dans les jardins de L'UQAM. La nouvelle espèce nord-américaine n'est

toujours pas nommée; des spécimens ont été envoyés au spécialiste des Myriapods Rowland M. Shelley (North Carolina Museum of Natural Science), mais il n'a pas été plus en mesure que moi de déterminer l'espèce. L'espèce fait partie de l'ordre des Chordeumatida et est distinctive par sa petite taille (~6.1 mm) et son nombre de segments (seulement 26 au stade adulte). Bien que relativement commune dans nos trois sites (88 spécimens capturés), elle est facilement confondue avec des immatures d'autres petits Chordeumatida. Seule la famille des Branneridae retrouvés dans le sud-est américain possède des espèces à 26 segments en Amérique du Nord, mais une vérification des gonopodes des mâles élimine facilement cette famille (Shear 2003a); même chose pour la famille européenne Brachychaeteumatidae qui possède également 26 segments, mais des gonopodes très différents (Blower 1986). Il pourrait donc s'agir d'une espèce non décrite; des spécimens seront envoyés à d'autres spécialistes prochainement. Selon la structure des gonopodes, la famille des Trichopetalidae me semble la plus probable, mais aucune espèce connue ne possède moins de 28 segments (Shear 2003b).

Les Chilopoda ont été très peu étudiés en Amérique du Nord et la seule clé d'identification disponible se limite à la faune du centre nord des États-Unis (Summers 1979) ce qui complexifie fortement leur identification; pour cette raison, mes spécimens n'ont pas tous pu être identifiés à l'espèce. Par contre, la faune du Québec est particulièrement peu étudiée; seulement quatre espèces sont répertoriées en milieu naturel (Mercurio 2010), mais le nombre réel est probablement au moins le triple. Dans mon projet 11 espèces et morpho-espèces ont été identifiées, mais dues à mes limites taxonomiques, seulement trois sûrs peuvent être ajoutée à liste des espèces du Québec (*Strigamia chionophila* (Wood), *Schendyla nemorensis* (Koch) et *Bothropolys multidentatus* (Newport)) et une potentielle (*Nadabius politus* Bollman) .

Les autres groupes étudiés sont mieux connus ou peu diversifiés et donc peu de nouvelles mentions supplémentaires ont été trouvées. Tout de même, pour les

Pseudoscorpionides, trois des quatre espèces identifiées seraient nouvelles pour le Québec selon la liste de Buddle (2010): *Pselaphochernes scorpionides* (Hermann), *Illinichernes distinctus* Hoffman et *Syarinus enhuycki* Muchmore. Chez les araignées (Araneae), on ajoute l'espèce *Zelotes duplex* Chamberlin (Gnaphosidae) et potentiellement *Disembolus corneliae* (Chamberlin & Ivie) (Linyphiidae). Chez les insectes, outre *O. pluricostatus*, nous ajoutons l'espèce de Thysanoptera *Merothrips floridensis* (Watson) et sa famille Merothripidae à la faune du Canada; l'identification a été confirmée par Eric Maw (Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa). Le genre *Thriscoptiloides* (Coleoptera: Ptiliidae) et également répertorié pour la première fois au Canada (la tribu Nanosellini est nouvelle pour le Québec); l'identification au genre a pu être confirmée par photo par le spécialiste Gene Hall (University of Arizona), mais malheureusement, le spécimen a été perdu par les services postaux entre Montréal et Tucson lorsqu'envoyé pour une identification à l'espèce! Finalement, chez les Hymenoptera, l'espèce *Dipara trilineatus* (Yoshimoto) (Pteromalidae) est également mentionnée pour la première fois au Canada.

Table 1.B Liste des espèces nouvelles pour le Québec trouver durant ce projet et leur répartition dans les sites échantillonnés: SB = St-Bruno, SH = St-Hilaire, MÉ = Mont-Écho, Au = Autre. Un '?' indique une identification incertaine.

Taxa	Famille	Espèce	SB	SH	MÉ	Au
Araneae	Gnaphosidae	*Zelotes duplex* Chamberlin	1			
	Linyphiidae	*Disembolus corneliae* (Chamberlin & Ivie)?		1		
Opiliones	Ceratolasmatidae	*Crosbycus dasycnemus* (Crosby)		1		
	Phalangiidae	*Lacinius* sp.?			18	
		Rilaena triangularis (Herbst)	5	3		
	Sclerosomatidae	*Leiobunum aldrichi* (Weed)	24	20		
		Leiobunum exilipes (Wood)?	1			
	Trogulidae	*Trogulus tricarinatus* (Linné)		15		
Pseudoscorpiones	Chernetidae	*Illinichernes distinctus* Hoffman	4	7		
		Pselaphochernes scorpionides (Hermann)	3	13		
	Syarinidae	*Syarinus enhuycki* Muchmore	2		2	
Diplopoda	Blaniulidae	*Choneiulus palmatus* (Nemec)				3
		Nopoiulus kochii (Gervais)	104			
	Julidae	*Cylindroiulus truncorum* (Silvestri)	2	1		
	Parajulidae	*Oriulus venustus* (Wood)	35	1		
	Polydesmidae	*Polydesmus denticulatus* Koch				1
		Pseudopolydesmus canadensis Newport			3	
	Trichopetalidae?	?	19	27	42	
Chilopoda	Linotaeniidae	*Strigamia chionophila* (Wood)	20	21	67	
	Lithobiidae	*Bothropolys multidentatus* (Newport)		1	3	
		Nadabius pullus Bollman?	2	1		
	Schendylidae	*Schendyla nemorensis* (Koch)	6	1		
Thysanoptera	Merothripidae	*Merothrips floridensis* (Watson)		1		
Coleoptera	Histeridae	*Onthophilus pluricostatus* (LeConte)	1			
	Ptiliidae	*Thriscoptiloides* sp.		1		
Hymenoptera	Pteromalidae	*Dipara trilineatus* (Yoshimoto)		4		

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